



Ferns of the Lower Jurassic from the Mecsek Mountains (Hungary): taxonomy and palaeoecology

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Abstract

Ferns are the most diverse group in the Early Jurassic plant assemblage of the Mecsek Mountains in southern Hungary and, considering their abundance and diversity, are an important element of the flora. Five families were recognized so far from the locality; these are, in order of abundance, the Dipteridaceae (48% of collected fern remains), Matoniaceae (25%), Osmundaceae (21%), Marattiaceae (6%) and Dicksoniaceae (three specimens). Ferns are represented by 14 taxa belonging to nine genera: *Marattiopsis hoerensis*, *Todites princeps*, *Todites goeppertianus*, *Phlebopteris angustiloba*, *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., *Matonia braunii*, *Thaumatopteris brauniana*, *Clathropteris meniscoides*, *Dictyophyllum nilssoni*, *Dictyophyllum rugosum*, *Cladophlebis denticulata*, *Cladophlebis haiburnensis*, *Cladophlebis roessertii*, and *Coniopteris* sp. Ferns from the Mecsek Mts. are rarely found in association with other plants. They co-occur mostly with leaves of *Nilssonia*, leaflets of *Sagenopteris*, and rarely with other plants. The most commonly co-occurring fern species is *P. kirchneri* Barbacka and Kustatscher sp. nov. According to our statistical approach (PCA, Ward cluster analysis), the fern taxa cluster in four groups corresponding to their environmental preferences, determined by moisture and disturbance. Most taxa grew in monospecific thickets in disturbed areas; a few probably formed bushes in mixed assemblages, whereas one taxon, *P. kirchneri*, probably was a component of the understorey in a stable, developed succession of humid environments.

Keywords Hettangian · Pteridophyta · Plant associations · Palaeobiogeography · Palaeoenvironment · Statistics

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Introduction

The Mecsek Mountains (southern Hungary) are well known for their mining activities since the nineteenth century (e.g., Hantken 1878; Barbacka 2011). These mining activities were developed on Triassic–Jurassic rocks near the city of Pécs, yielding thousands of plant remains (e.g., Beudant 1822; Barbacka 2011). Systematic collecting of

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plant remains has been carried out since 1989 (e.g., Barbacka 1991, 1994a, b, 2001, 2002, 2009). Palaeobotanical studies include basic taxonomy (e.g., Barbacka 1991, 1994a, b, 2009; Barbacka and Bóka 2014), considerations on intraspecific variability of plants (e.g., Guignard et al. 2001; Barbacka and Bodor 2008; Bodor and Barbacka 2008) and palaeoecological/palaeoenvironmental reconstructions (Barbacka 2011; Barbacka et al. 2014). The palaeoecology was based on preferences of the plant remains (more than 700 slabs) regarding the co-existence of taxa on the same slabs, the paleoenvironment was inferred from taxa connected to selected lithologies and their spatial distribution.

The flora comprises at least 55 taxa of leaves, reproductive organs, seeds or trunks belonging to all major plant groups (Barbacka 2011) and shows a higher variability on higher systematic level (families or genera) than on species level. Fern remains are very common, with a higher relative abundance than relative species richness. They are usually considered indicators for humid environments because their reproductive cycle is strongly linked to moisture (at least the gametophytes) although some extant ferns are adapted also to more arid environments (Van Konijnenburg-van Cittert 2002 and ref. therein). This has been observed also in some fossil ferns of Hungary (Barbacka 2011).

The aim of this study is to increase our comprehension of the biodiversity of the Jurassic flora of the Mecsek Mountains by unraveling one of its main components, the ferns. Co-occurrence analyses of ferns with other plant groups gives insights into Jurassic biocoenoses. The flora from the Mecsek Mountains is a good object for such a study since its plant assemblages can be considered (par-)autochthonous (e.g., Barbacka 2011), permitting us to determine the palaeoecological preferences of single taxa and to reconstruct the palaeoenvironmental conditions the plants grew in.

Geology, materials and methods

Jurassic sediments rich in plant macrofossils are confined in Hungary to the coal-bearing horizons of the Mecsek Coal Formation (Hetényi in Császár 1997) of the Mecsek Mountains (Baranya County, southern Hungary; Fig. 1). The coal seams of the Mecsek Coal Formation are Hettangian in age (Góczán 1956; Földi 1967; Paál-Solt 1969; Nagy and Nagy 1969; Szente 1992; Landis et al. 2003), although, thin coal seams appear already in the fluvial succession of the latest Rhaetian (Hetényi in Császár, 1997). During the Early Jurassic, a fluvial-lacustrine-palustrine environment was formed, and paralic coal-swamp deposits became dominant. Plant beds alternate occasionally with mollusc-bearing marine sublittoral layers. Crinoids appear in the upper part of the formation, indicating open marine conditions. The coal-bearing area extends in N–S direction, over a distance of

about 20–30 km, from Nagymányok to Pécs, constituting a mining region of 350–400 km². The sedimentary succession might change in facies within the same locality (shafts and open mines) and within short distances due to tectonic activity and strong subsidence (Nagy and Nagy 1969). Unequal (synsedimentary) subsidence caused differences in thickness and carbonization degree of the various coal deposits (Nagy and Nagy 1969) with a lowest thickness near Nagymányok (120 m), increasing gradually southward (Pécs; 1000–1200 m thick, for more details see Barbacka 2011).

Mining activities in the Mecsek Mountains have been ongoing for more than 200 years with an intense exploration period between 1960 and 1990. In 2004 the underground mines were closed and open mining stopped. More than 5000 rock slabs with plant fossils were collected in the years 1989–2004 by one of the authors (MB); 805 fern remains were identified and used for this study. They are represented generally by frond fragments, often of large dimensions. The specimens are preserved in siltstone, shaly siltstone, fine detritic siderite and carbonate sandstone (Bodor and Barbacka 2008). Most frond fragments are preserved as impressions; (highly) coalified organic material is rare. Details are well visible in the fine sediments, although in situ spores are not preserved.

The plant fossils originate from different sites all over the Mecsek Mountains, both from open cast mines (e.g., Pécs-Vasas, Pécsbánya) and dumps of deep shafts (e.g., Béta, Zobák or Kossuth). Since the specimens were not collected in situ, although this does not influence the character of the material, a collecting bias cannot be completely excluded. However, the fact that all plant fossils have been collected by the same person (MB), excludes a difference in collecting method between the different plant sites. The collection of plant fossils is deposited in the Botanical Department of the Hungarian Natural History Museum in Budapest and labelled with inventory numbers preceded by prefix BP. Since the fern material was preserved without cuticles, the macroscopic features were studied using an Olympus SZX9 stereo microscope. Pictures were taken with a Nikon 800E, objective Nikkor 60 mm micro, in double polarized light.

Fern taxonomy, intraspecific variability and plant co-occurrence were studied. For the latter, a database was constructed showing all co-occurrences between fern remains and other plant fossils on the same rock slabs. These provide important insights into taxa co-occurring within the same habitats, since the plant assemblage can be considered (par-) autochthonous. *Coniopteris* sp. is the only taxon missing in the statistical analyses because it is represented by three specimens only.

Co-occurrences were studied with statistical methods. Data were collected from both sides of the slabs and they were treated separately. In some cases, the state of

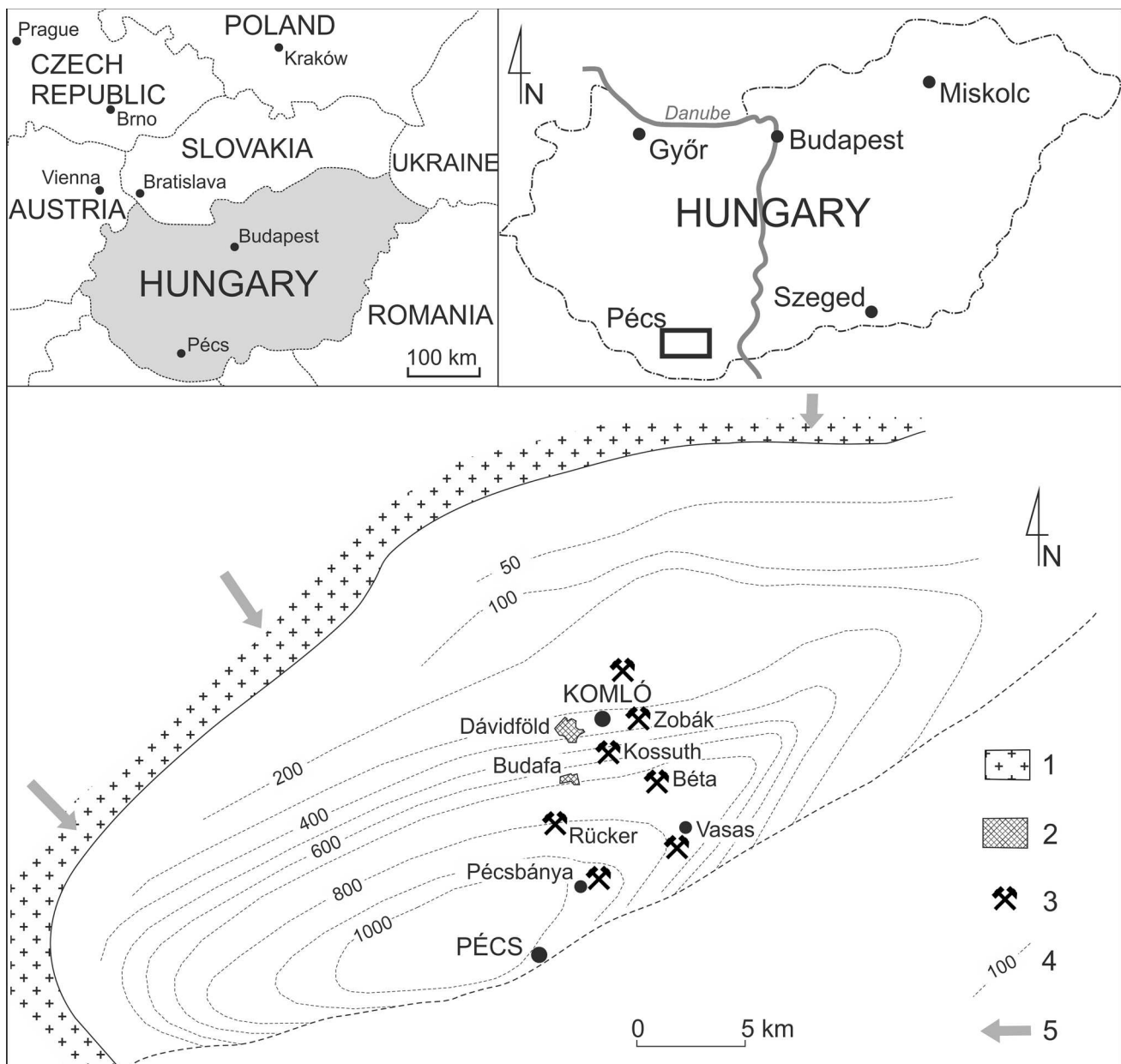


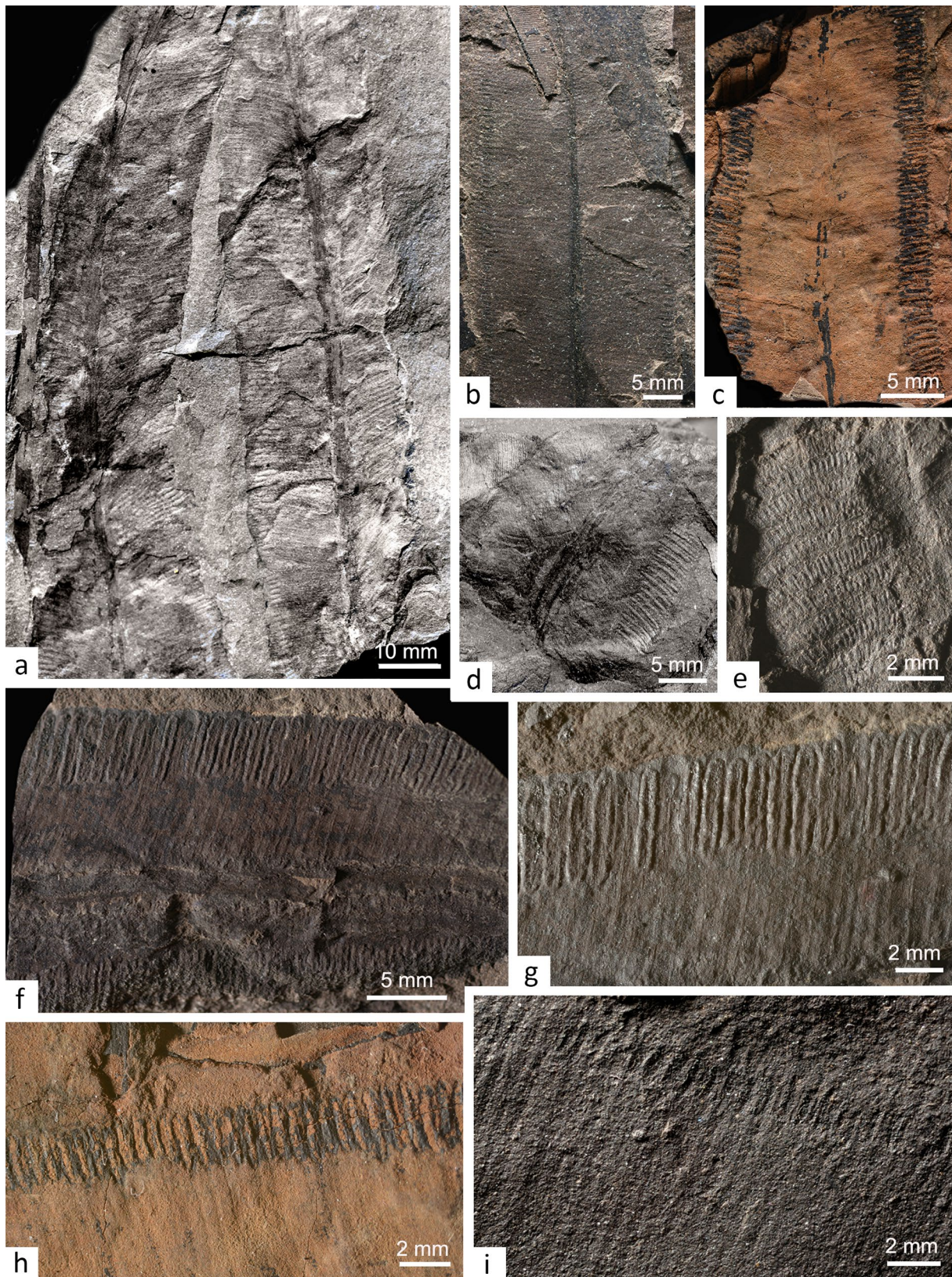
Fig. 1 Map of the localities and sedimentary basin in the Mecsek Mts., Hungary. **1** Granitoid denudated area (sedimentary basin margin), **2** Dumps, **3** Coal mines, **4** Isolines of hypothetical basin thickness, **5** direction of granitoid clast transport

preservation and fragmentation of the remains was too poor for a specific determination; in this case, the data were considered at a generic level. The database comprehends a total of 903 records (S1—the complete database is given in the supplement to this paper). For the statistical and mathematical analyses the programs R (R Core Team 2011) and PAST (Hammer et al. 2001) were used. The data were appropriate for an integration of cluster analysis and ordination that is suggested to be applied to the same data for palaeoecological purposes (Shi 1993).

Multivariate analytical methods were used to analyse the data, a hierarchical grouping and an ordination to detect the background affecting factors.

The purpose of the cluster analysis used in this study is to discover the system of organization of groups in which the members share common properties (Kovács et al. 2012).

The advantage of Ward's method is that it minimizes the total within-cluster variance. It is widespread used in



◀**Fig. 2** *Marattiopsis hoerensis* (Schimper) Thomas 1913. **a** Two typical sterile pinnules, with distinct venation, No. 92.262.1; **b** Detail of fertile pinnule with short synangia (immature?) No. 96.334.1. (photo MS); **c** Detail of fertile pinnule with short synangia (old?) No. 2017.53.1. (photo MS); **d** Base of a fertile pinnule, No. 98.496.1; **e** Synangia under high magnification showing sporangia, No. 96.72.1. (photo MS); **f** Detail of fertile pinnule with fully developed synangia, No. 94.551.1. (photo MS); **g** Detail of **f** showing the arrangement and dimension of the synangia (photo MS); **h** Detail of **c** showing the arrangement and dimension of the synangia (photo MS); **i** Detail of **b** showing the arrangement and dimension of the synangia (photo MS)

paleontology and in palaeoecology (Chabrerie et al. 2003; Currano et al. 2010; Teodoridis et al. 2011; Barbacka et al. 2014).

Principal component analysis (PCA) was conducted on the variance–covariance matrix for detecting the background factors influencing the vegetation groups. The joint distribution of the species along the orthogonal axes of PCA analysis may give a rough estimation of their ecological profiles. This method is commonly used in palaeobotany since Spicer and Hill used it in 1979 (Spicer and Hill 1979) and gave a good results in the palaeoecological analysis of Jurassic flora from Mecsek (Barbacka et al. 2016). The effectiveness depends on the original correlation values among the variables. If many variables are correlated, the first component would explain a high percentage of variance (Barbacka et al. 2014; Kovács et al. 2012). The number of principal components is less than or equal to the number of original variables (see also Supplement, S3).

Systematic palaeontology

Order **Marattiales** Link 1833

Family **Marattiaceae** Kaulf 1824

Genus ***Marattiopsis*** Schimper 1869

Marattiopsis hoerensis (Schimper) Thomas 1913

Figure 2a–i

Selected synonyms.

- 1869 *Angiopteridium hoerense*—Schimper: p. 604, pl. 38, fig. 7.
- ? 1869 *Angiopteridium muensteri* (Göppert)—Schimper: p. 603, pl. 35, figs. 1–6.
- 1913 *Marattiopsis hoerensis* (Schimper)—Thomas: p. 229.
- ?1913 *Marattiopsis anglica*—Thomas: p. 228, pl. 23, figs. 1–3, text-fig. 1.

- 1919 *Marattiopsis hoerensis* (Schimper) Thomas—Antevs: p. 21, pl. 2, figs. 2–13, pl. 6, fig. 40.
- 1924 *Marattiopsis hoerensis* (Schimper) Thomas—Chow: p. 5, pl. 2, figs. 2–3.
- 1931 *Marattiopsis hoerensis* (Schimper) Thomas—Harris: p. 60, pl. 13, figs. 2, 3, 5, 6, 9–11, 15, 16, text-figs. 21–22.
- ?1961 *Marattia anglica* (Thomas)—Harris: p. 72, text-fig. 23.
- ?1974 *Marattiopsis muensteri* (Göppert)—Schimper: p. 514.
- 2002 *Marattiopsis hoerensis* (Schimper) Thomas—Van Konijnenburg-van Cittert: p. 115.
- 2011 *Marattia hoerense* (Schimper) Harris—Kiritchkova and Nosova: p. 51, pl. 9, fig. 10, pl. 11, figs. 1–2.

Description. The fronds are pinnate with linear pinnae (15–40 mm wide) decreasing in size towards the apex. No entire pinna is preserved; the longest fragment reaches 180 mm in length. The base of the pinnae is slightly expanded (Fig. 2d), nearly cordate, the margins are entire; no pinna apex is preserved. The midrib is 1–7 mm, most frequently 4 mm, wide. Lateral veins are generally poorly visible, parallel, sometimes forking once at the midrib, and reaching the margins at almost right angle. The number of veins varies (9–17 per 10 mm, in most cases 10–12 per 10 mm). Synangia are 2–10 mm long and arranged perpendicularly to the pinna margin; their number corresponds to the number of lateral veins. The pinnae width/synangia length ratio ranges from 5 to 29%. Synangia may be of two types. Synangia type 1 are elongated with rounded ends, about 0.8 mm wide with neighbouring synangia touching each other; a central double line indicates the slit (Fig. 2f, g). Synangia type 2 are spindle shaped with rather acute ends and a width of about 0.5 mm; they do not touch and the central line is not recognizable (Fig. 2h, i). The number of sporangia is not clear in both synangia types (Fig. 2e).

Remarks. The genus *Marattiopsis* has been created by Schimper (1869) for extinct taxa resembling species of the extant genus *Marattia* O. Swartz 1788 (e.g., Bomfleur et al. 2013; Escapa et al. 2015). The pinna width to synangia length ratio (PW/SL), venation pattern and morphology of the pinna base are considered the most important features for the distinction between different species within *Marattiopsis* (e.g., Harris 1931, 1961; Kvaček 2014; Escapa et al. 2015), especially morphologically close species such as *M. hoerensis* (Schimper) Thomas 1913, *M. muensteri* (Göppert) Schimper 1874, and *M. anglica* Thomas 1913, *M. asiatica* Kawasaki 1939, *M. crenulata* Lundblad 1950 and *M. angustifolia*.

The frond fragments from the Jurassic of Hungary are mostly preserved as central pinnae fragments with only one

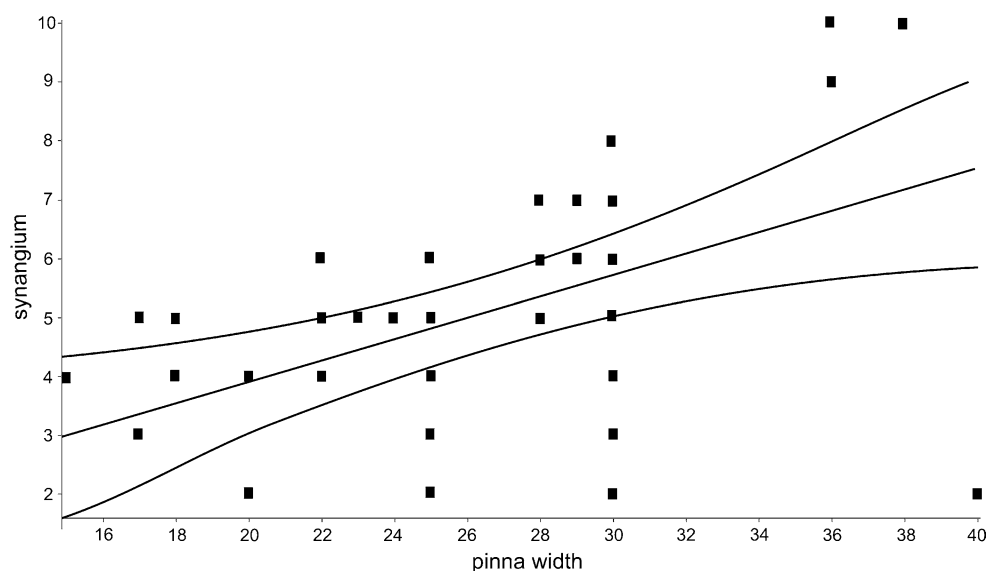


Fig. 3 Linear regression of leaf width/synangia length ratio in the Hungarian *Marattiopsis hoerensis* (Schimper) Thomas 1913 specimens

basal frond fragment. The pinnae fragments can be distinguished based on their synangia shape and dimension in two groups (ST1 and ST2), despite having the same venation pattern and pinna size. The PW/SL ratio, calculated for all well enough preserved specimens (about 70% of the frond fragments), show a continuous data set between the lowest and highest values (5–29%; Figs. 3, S2). There is no significant difference between both groups of pinnae (ST1 and ST2). They tend a little to association of wider pinnae with longer synangia, but not strongly. The extreme values also are still within the curve limit. Since the pinnae are often fragmentarily preserved and features such as the shape of the base or of the entire pinna are lacking, the PW/SL ratio is considered as a convenient and easily available character for taxonomical classification. However, the variability observed in the rich Hungarian material casts some doubts on the usefulness of this criterion for specific determinations.

Moreover, different stages in the synangia development of extant Marattiaceae (Senterre et al. 2014) correspond to different synangia types observed in *M. hoerensis* from Hungary. Small oval or slightly elongated immature synangia on extant fronds have a similar PW/SL ratio as fossil specimens with ST1. Mature synangia are much longer and wider, whereas old ones decrease in size and become spindle-shaped, but do not show any median slit, similar to ST2. This highly suggests that the observed differences in PW/SL ratio correspond to different stages of synangia development. Antevs (1919) described similar differences in synangia type, with mature long synangia (Antevs 1919, pl. 2, fig. 3) and young short synangia (Antevs 1919, pl. 2, fig. 4a) from the Late Triassic–Early Jurassic flora of Sweden.

Marattiopsis hoerensis differs from other species because of its PW/SL ratio, the expanded, cordate base, the basal veins turning backward and the reducing pinna size from the base to the apex. These features, apart from the basal veins, which are not visible, allow us to classify the Hungarian specimens as *M. hoerensis*. However, if the PW/SL ratio is linked to the developmental stages of the synangia as suggested above, then the differences between *M. hoerensis* and other similar species (Harris 1931, 1961) are reduced to mere details. In that case, *M. muensteri* differs because of its rounded, but not expanded base, *M. crenulata* because of its crenulate margin and *M. asiatica* because of the higher density of veins forking in the lamina. Kilpper (1964), proposed to fuse *M. hoerensis*, *M. muensteri*, *M. anglica*, *M. crenulata* into one species, *Marattiopsis intermedia* (Münster) Kilpper, 1964, arguing that there is an overlap between all these species. Van Konijnenburg-van Cittert (1975, p. 209, tab. 1) agreed that the species were rather alike, but considered the overlap a result of comparing small distal pinnules from one species with large proximal ones of another species, even admitting that in some floras there might exist frond fragments with intermediate pinnae.

Comparing pinnae shape and their bases in some extant marattiales (e.g., *Marattia fraxinea* J. Sm. ex Gmel. 1924, *M. sorbifolia* Swartz 1806, *M. laxa* Kunze 1844), these seem to vary along the rachis. Bases in pinnae are more strongly asymmetric at the top and become more symmetric towards the basis of the frond; the lowermost may be plain or lobed. Such a high variability within single herbarium specimens could indicate that some of the differences in shape may be caused by environmental conditions or plain variability. Thus, it cannot be excluded that the four species discussed

by Harris (1931), *M. hoerensis*, *M. asiatica*, *M. crenulata* and *M. angustifolia*, are conspecific, as suggested by Kilpper (1964).

The in situ spores of *M. hoerensis* are known as monolete and oval to bean-shaped, about 28 µm long, with a thick and finely granulate wall (Harris 1931; Lundblad 1950; Van Konijnenburg-van Cittert 1975). These belong to the dispersed spore genus *Punctatosporites* Ibrahim 1933. Few in situ spores were trilete (less than 1%) with long laesurae (Van Konijnenburg-van Cittert 1975), corresponding to the dispersed genus *Granulatisporites* Ibrahim, 1933. However, Götz et al. (2011, tab. 2) did not identify these two genera among the dispersed spores of the Upper Triassic–Lower Jurassic sediments of Hungary. *M. hoerensis* was distributed from the Rhaetian to Lower Jurassic in Europe (Table 1).

Material. The species is represented by fertile pinnae fragments; only few specimens are preserved as well. BP 89.157.1, 94.433.1, 94.551.1, 96.52.1, 96.57.1–58.1, 96.67.1–74.1, 96.76.1, 96. 78.1, 96.172.1, 96.262.1, 96.325.1, 96.334.1, 96.480.1–482.1, 98.356.1–359.1, 98.426.1, 98.470.1, 98.513.1–520.1, 2006.661.1–665.1, 2007.139.1, 2007.806.1, 2007.910.1 (46 specimens)

Order **Osmundales** Link 1833

Family **Osmundaceae** Martinov 1920

Remarks. The Hungarian Jurassic species of *Todites* and *Cladophlebis* were extensively described and discussed in Barbacka and Bodor (2008). Here we provide the same descriptions supplemented by brief remarks in order to give a complete overview on all fern taxa from the locality. *Todites* is a fossil genus for fertile osmundaceous fronds, *Cladophlebis* for sterile fronds of which fertile units often belong to the osmundaceous genera *Todites* or *Osmundopsis* (Harris 1961; Van Konijnenburg-van Cittert 1996). However, this distinction is not strictly followed, since *Cladophlebis* species with sporangia have been described (Nathorst 1878; Watson 1969), as well as *Todites* species without sporangia (Seward 1911; Oishi 1939–1940; Kräusel 1958; Van Konijnenburg-van Cittert and Van der Burgh 1989). Harris (1961) suggested close relationships between both genera within the family Osmundaceae, a consideration we follow for our *Cladophlebis* and *Todites* species of the Jurassic of Hungary (Barbacka and Bodor 2008).

Genus ***Todites*** Seward 1900

Todites princeps (Presl in von Sternberg) Gothan 1914
Figure 4a

Selected synonyms (for more details see Schenk 1867; Harris 1931, 1961; Schweitzer 1978; Barbacka and Bodor 2008).

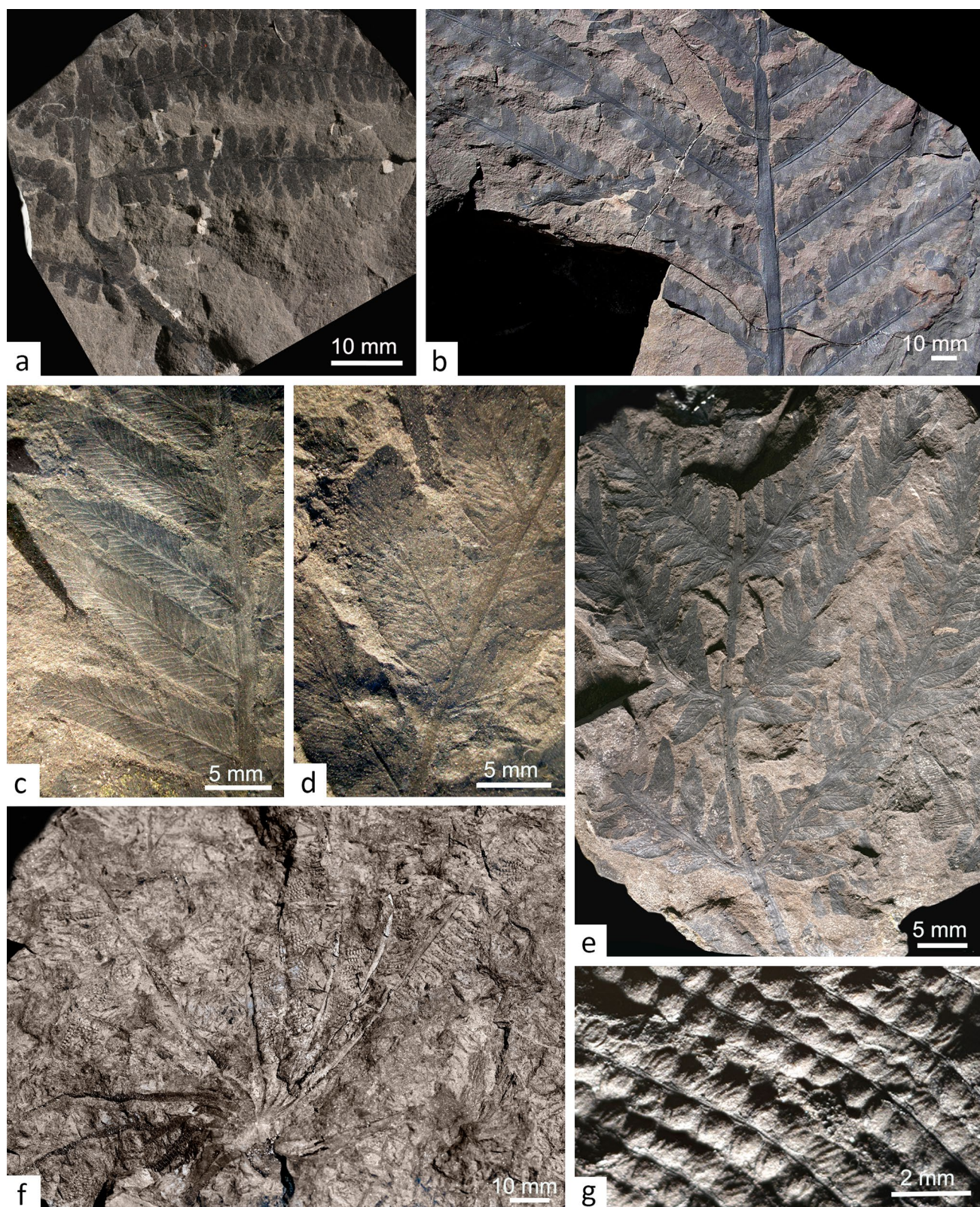
- 1838 *Sphenopteris princeps*—Presl in von Sternberg: p. 126, pl. 59, figs. 12–13.
- 1867 *Acrostichites princeps* Presl—Schenk: p. 46–49, pl. 7, figs. 3–5, pl. 8, figs. 1, 1a.
- 1931 *Todites princeps* (Presl) Gothan—Harris: p. 35–39, pl. 11, figs. 1, 2, 4, 9, pl. 12, fig. 3, text-figs. 8–9.
- 1961 *Todites princeps* (Presl) Gothan—Harris: p. 93–99, text-figs. 30–31.
- 1978 *Todites princeps* (Presl) Gothan—Schweitzer: p. 31–36, pl. 1, figs. 3–5, pl. 2, figs. 1–6, pl. 3, figs. 1–7, text-figs. 10–18.
- 2008 *Todites princeps* (Presl) Gothan—Barbacka and Bodor: p. 134, pl. 1, figs. 1–5.
- 2008 *Todites princeps* (Presl) Gothan—Bodor and Barbacka: p. 212.

Description (after Barbacka and Bodor 2008; Bodor and Barbacka 2008). Fronds are bipinnate in an anadromic way, with similar sterile and fertile fronds. The rachis is 1.5–4.5 mm wide and smooth. Pinnae reach more than 60 mm in length (no complete pinnae are preserved). The rachis of the pinnae is 0.5–0.8 mm wide. Pinnules are attached alternately or oppositely, arising from the rachis at about 90° (with their angle decreasing slightly towards the top of the pinna). Pinnules are variable in shape and size, margins are mostly entire to crenate to deeply lobed. They are 4–10 mm long and 2–4 mm wide. Their apex is usually rounded. Circular sporangia are attached densely on the lower surface of the pinnules.

Remarks. The pinnule size and shape vary noticeably in this species depending on the position of the pinnae on the fronds (Harris 1931, 1961; Barbacka and Bodor 2008; Bodor and Barbacka 2008). In the Hungarian material in situ spores could not be extracted; however, they are well known from the Jurassic of Yorkshire (Harris 1961). The spores are supposed to be roundish (20–40 µm diameter) with a smooth wall and a distinct trilete mark that is smaller than the radius of the spores. This spore type belongs to the dispersed spore genus *Todisporites* Couper 1958, represented in the Upper Triassic–Lower Jurassic sediments of Hungary by *Todisporites major* Couper 1958 and *T. minor* Couper 1958 (Götz et al. 2011). The latter might represent the in situ spores of *T. princeps*.

Material. BP 94.187.1, 94.190.1, 94.192.1, 94.194.1, 94.485.1–486.1, 94.690.1–692.1, 94.710.1–711.1, 2008.421.1–423.1 (44 specimens).

Todites goeppertianus (Münster in Göppert) Krasser 1922
Figure 4b



◀**Fig. 4** Ferns of the Early Jurassic of Hungary. **a** Frond fragment of *Todites princeps* (Presl in von Sternberg) Gothan 1914, No. 94.692.1. (photo MS); **b** Frond fragment of *Todites goeppertianus* (Münster in Göppert) Krasser 1922, No. 89.224.1; **c** Pinna fragment of *Cladophlebis denticulata* (Brongniart) Fontaine, 1899, No. 2004.1040.1; **d** Pinna fragment of *Cladophlebis haiburnensis* (Lindley and Hutton) Brongniart 1849, No. 89.194.1; **e** Frond fragment of *Cladophlebis roessertii* (Presl in von Sternberg) Saporta 1873, No. 2004.968.1. (photo MS); **f** Basal frond fragment of *Phlebopteris angustiloba* (Presl in von Sternberg) Hirmer and Hörhammer 1936, No. 89.440.1. (photo MS); **g** Venation pattern of *Phlebopteris angustiloba* (Presl in von Sternberg) Hirmer and Hörhammer 1936, No. 94.474.1. (photo MS)

Selected synonyms (for more details see Schenk 1867; Harris 1931; Barbacka and Bodor 2008).

- 1846 *Neuropteris goeppertiana*—Münster in Göppert: p. 104, pl. 8, 9, figs. 8–10.
- 1867 *Acrostichites goeppertianus*—Schenk: p. 44–46, pl. 5, figs. 5, 5a.
- 1922 *Todites goeppertiana* (Münster) Krystofovitsch—Krasser: p. 355.
- 1931 *Todites princeps* (Presl) Gothan—Harris: p. 31–35, pl. 11, figs. 3, 8, text-fig. 7.
- 2008 *Todites goeppertianus* Krasser—Barbacka and Bodor: p. 134–135, pl. 1, figs. 6–9, pl. 2, figs. 1–4.
- 2008 *Todites goeppertianus* Krasser—Bodor and Barbacka: p. 212, figs. 26A–J.

Description (after Barbacka and Bodor 2008). Fronds are bipinnate and large with sterile and fertile leaves representing different morphotypes. The sterile morphotype has a smooth primary rachis (< 20 mm) from which arise the pinnae at about 45°. Pinnules are inserted oppositely, close to each other, but not overlapping the pinna rachises (1.5–3.0 mm wide). They are linear to falciform, 5–10 mm long and 2.5–6.0 mm wide. The bases are broad, sometimes acroscopically slightly extended, and usually touching the neighboring pinnules. The margins are entire, the apex subacute to rounded. Venation is of neuropterid-type, secondary veins fork once. Fertile fronds are large with a 20 mm wide primary rachis and an up to 3 mm wide pinna rachis. Pinnules are often falciform, 5–8 mm long and 3.0–4.5 mm wide, not touching the neighboring pinnules. The margins are entire with a rounded apex, the venation is of neuropterid-type. Sporangia cover the entire lower side of the pinnules; they are globose and about 0.25–0.3 mm in diameter. In situ spores are trilete, about 40 µm in diameter.

Remarks. This species differs from other species from this genus due to its characteristic neuropterid venation (pecopterid venation in the other taxa; Barbacka and Bodor 2008). For a more detailed discussion see Barbacka and Bodor

(2008). Krasser (1922, p. 355) indicated „Krystof.” as author of the combination “*Todites goeppertiana*” without giving any references to the paper of Krystofovich. However, later most authors referred this combination to Krasser (1922).

Material. BP 60.150.1, 89.179.1, 89.254.1–264.1, 89.266.1, 89.448.1, 89.452.1, 89.457.1, 94.188.1, 94.210.1, 94.222.1, 94.226.1–227.1, 94.437.1, 94.440.1, 94.444.1, 94.489.1, 94.517.1, 94.616.1–631.1, 94.633.1–635.1, 94.728.1, 94.798.1, 96.127.1, 96.137.1R, 96.338.1, 96.341.1, 98.351.1, 96.384.1, 96.386.1, 98.763.1, 98.1003.1, 2000.1168.1, 2004.1182.1, 2005.644.1, 2006.663.1R, 2006.681.1–682.1, 2007.155.1, 2007.175.1, 2009.465.1 (55 specimens).

Genus *Cladophlebis* Brongniart 1849

Cladophlebis denticulata (Brongniart) Fontaine 1899
Figure 4c

Selected synonyms (for more details see Harris 1961; Barbacka and Bodor 2008).

- 1828a *Pecopteris denticulata* Brongniart—Brongniart: p. 57 (*nomen nudum*).
- 1828a *Pecopteris denticulata* Brongniart—Brongniart: p. 301, pl. 98, figs. 1–2.
- 1899 *Cladophlebis denticulata* Brongniart—Fontaine: p. 71, pl. 4, fig. 2, pl. 7, fig. 7.
- 1931 *Todites denticulatus* (Brongniart) Krasser—Harris: p. 48, pl. 9, figs. 9–10.
- 1961 *Todites denticulatus* (Brongniart) Krasser/*Cladophlebis denticulata* (Brongniart) Fontaine—Harris: p. 79–87, text-figs. 25–27.
- 1961 *Phlebopteris braunii* (Göppert) Hirmer et Hörhammer—Nagy: p. 618, pl. 9, fig. 3.
- 1997 *Cladophlebis denticulata* ((Brongniart) Fontaine—Popa: fig. 30.
- 2002 *Cladophlebis denticulata* (Brongniart) Fontaine—van Konijnenburg-van Cittert: p. 115, pl. 1, fig. 3.
- 2008 *Cladophlebis denticulata* (Brongniart) Fontaine—Barbacka and Bodor: p. 135–138, pl. 2, figs. 5–9.
- 2008 *Cladophlebis denticulata* (Brongniart) Fontaine—Bodor and Barbacka: p. 212, figs. 25A–G.

Description (after Barbacka and Bodor 2008). Fronds are bipinnate with a ridged or smooth rachis of 1–4 mm width. Pinnae are attached oppositely, alternately or subalternately with an angle of 27°–65° that decreases slightly towards the top of the frond. Pinnules arise oppositely, semi-alternately or alternately. They are elongated (length/width ratio = 1.5–4.6), often falcate, 7–28 mm long and 3–9 mm wide. The margin of the pinnules is generally dentate, but

partly dentate or entire margins are not rare. The apex is acute or subacute, its base as wide as the pinnules or slightly extended acroscopically. The veins are distinct; the midrib reaches the apex of the pinnule; secondary veins divide once or twice, often only in the basal part of pinnules. The number of secondary veins on each half pinnule varies from 4 to 14, the vein density at the margin is 3–9/cm.

Remarks. Harris (1961) suggested to use the name *T. denticulatus* (Brongniart) Krasser 1922 for fertile fronds and *C. denticulata* for sterile frond fragments and van Konijnenburg-van Cittert (1996) has demonstrated that the sterile fronds can actually belong to two different fertile taxa, respectively *T. denticulatus* and *Osmundopsis sturii* depending on the morphology of their fertile parts. Since our specimens are all sterile we use in this study the name *C. denticulata*. *C. denticulata* is easily distinguished from the other *Cladophlebis* species of Hungary due to its elongate pinnules with dentate margin, (sub)acute apex and ridged rachis (for a detailed discussion see Barbacka and Bodor 2008). The species is characterized by a high variability in shape and dimension of the pinnules that has been related to environmental adaptations (Barbacka and Bodor 2008; Bodor and Barbacka 2008). The specimen described by Nagy (1961) as *P. braunii* belongs to *C. denticulata*.

The macroremains of this species were found from the Late Triassic to the Cretaceous (Bodor and Barbacka 2012) of the entire world (Tab. 1). The in situ spores of *T. denticulatus* are roundish (25–48 µm diameter) with a thin, punctate wall and a delicate trilete aperture that extends over the entire radius (Harris 1961). This spore type belongs to the dispersed spore genus *Punctatisporites* Ibrahim 1933. The latter has not been mentioned so far from the palynological record of the Upper Triassic (Rhaetian) and Lower Jurassic (Hettangian) Mecsek Coal Formation (Götz et al. 2011).

Material. BP 91.113.1, 94.6.1, 94.35.1, 94.213.1, 94.435.1, 94.438.1, 94.438.1R, 94.450.1, 94.552.1, 94.704.1, 96.75.1, 96.123.1–125.1, 96.125.1R, 96.127.1–129.1, 96.317.1, 96.333.1, widespread species in the Jurassic 96.339.1, 96.350.1, 96.389.1, 96.390.1, 96.395.1, 96.397.1, 96.403.1, 96.504.1, 98.4.1, 98.1050.1–1051.1, 98.1074.1, 98.1177.1, 98.340.1, 2002.5.1, 2002.18.1, 2002.134.1, 2002.1004.1–1007.1, 2004.1001.1, 2004.1003.1–1011.1, 2004.1015.1, 2004.1021.1, 2004.1109.1, 2004.1183.1, 2004.1200.1, 2004.966.1, 2004.967.1, 2004.969.1–973.1, 2004.977.1–979.1, 2004.982.1, 2004.983.1, 2004.986.1, 2004.986.1R, 2004.988.1, 2004.991.1, 2004.995.1, 2004.999.1, 2005.830.1, 2005.840.1–844.1, 2005.863.1, 2006.683.1 (75 specimens).

Cladophlebis haiburnensis (Lindley and Hutton) Brongniart 1849

Figure 4d

Selected synonyms (for more details see Harris 1961; Barbacka and Bodor 2008).

- 1836 *Pecopteris haiburnensis*—Lindley et Hutton: p. 97, pl. 187.
- 1849 *Cladophlebis haiburnensis* (Lindley et Hutton)—Brongniart, p. 105.
- 1997 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart—Popa: fig. 25.
- 1997 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart—Barbacka and Bodor: p. 138–139, pl. 2, figs. 10–13.
- 1997 *Cladophlebis haiburnensis* (Lindley et Hutton) Brongniart—Bodor and Barbacka: p. 212, figs. 25H–L.

Description (after Barbacka and Bodor 2008). The frond is bipinnate with a slender main rachis that is up to 2.5 mm wide, and smooth. The primary rachises are oppositely inserted and about 1.0–1.5 mm wide. Pinnules arise alternately or oppositely, 6–18 mm long and 3–8 mm wide (max. 25 × 10 mm). They are lanceolate (length/width ratio 2–3), straight or falcate, depending on its position along the frond, with an entire margin and a subacute apex. Pinnules are attached to the rachis with the entire basis, which may be acroscopically extended. Adjacent pinnules touch each other or are divided by an interval of about 1 mm. Venation is of pecopterid type, with straight midvein and secondary veins forked once or twice. The number of veins on half of the pinnule is 4–11, vein density ranges from 7 to 28 veins/cm; the arising angle of the secondary veins is 16°–64°.

Remarks. *Cladophlebis haiburnensis* is one of the most widespread species in the Jurassic (e.g., Barbacka and Bodor 2008; Bodor and Barbacka 2012). It resembles *C. denticulata* due to its high variability in morphology (pinnules size, number of secondary veins) nonetheless both species are well distinguished from each other (Barbacka and Bodor 2008).

Material. BP 89.4.1, 89.186.1, 89.346.1, 94.223.1, 94.229.1, 94.436.1, 94.436.1R, 94.637.1, 94.720.1, 96.337.1, 96.345.1–346.1, 96.385.1, 96.391.1, 96.409.1, 98.1073.1, 98.762.1, 2001.625.1, 2004.975.1–976.1, 2004.980.1, 2004.989.1, 2004.990.1, 2004.1017.1 (24 specimens).

Cladophlebis roessertii (Presl in von Sternberg) Saporta 1873

Figure 4e

Selected synonyms (for more details see Schenk 1867; Gothan 1914; Barbacka and Bodor 2008).

- 1838 *Alethopteris roessertii*—Presl: p. 145, pl. 33, figs. 14a, b.
 1867 *Asplenites roessertii* Presl in von Sternberg—Schenk: p. 49–53, pl. 7, figs. 6–7, 7a, pl. 10, figs. 1–4.
 1873 *Cladophlebis roessertii* (Schenk)—Saporta: p. 301, pl. 31, fig. 4.
 1926 *Cladophlebis roessertii* (Schenk non Presl) Saporta—Harris: p. 57–59, text-figs. 3A–D.
 2008 *Cladophlebis roessertii* (Schenk) Saporta—Barbacka and Bodor: p. 138–139, pl. 2, figs. 10–13.
 2008 *Cladophlebis roessertii* (Schenk) Saporta—Bodor and Barbacka: p. 212, figs. 25H–L.

Description (after Barbacka and Bodor 2008). Fronds are slender and probably bipinnate, the fragments are up to 55 mm long. The main rachis is 1.5 mm wide, the pinna rachis 0.5–0.8 mm wide. Pinnae are inserted oppositely with a distance between neighboring pinnae of 15 mm. Pinnules are inserted oppositely; they are triangular with an acute apex and a relatively wide base, or rarely rectangular with a rounded apex; near the apex are the pinnules falcate. The adjacent bases touch each other. The pinnules are up to 18×6 mm (at the base of the pinna), but generally 6–7×3–4 mm. The venation is of pectopterid type, secondary veins are forked mostly once, occasionally twice. The number of veins at the margin of pinnule is usually 5–11, vein density is 8–13 veins/cm.

Remarks. There seems to be some confusion on the authorship of this taxon. Although Schenk (1867) clearly states that he considers his material belonging to the same species as Presl in von Sternberg (1820–1838, p. 145), later authors, including Harris (1926), base their identification on Schenk's paper (1867), pointing out that Presl's specimen is indeterminable and differs from Schenk's material, and thus, use Schenk as official author of the taxon (followed also by Barbacka and Bodor 2008). Since Presl in von Sternberg (1820–1838) is, however, the first to use of the name, Schenk's name would be a later homonym, if he did not expressly refer to Presl's species. Thus the correct first author is Presl in von Sternberg (1820–1838). Saporta (1873) moved the species to *Cladophlebis*, while Gothan (1914) ascribed it to *Todites*, indicating, however, that Kryztofovich (1912) had already proposed the new combination. Since we do not have any fertile material in Hungary, we use the sterile version *Cladophlebis* following Harris (1961). The species is well represented in the Late Triassic to Cretaceous around the globe (Table 1).

Material. BP 2004.19.1, 2004.968.1, 2004.974.1, 2004.981.1, 2004.984.1–985.1, 2004.987.1, 2004.990.1, 2004.992.1–998.1, 2005.839.1, 2004.1000.1, 2004.1014.1, 2004.1017.1R, 2004.1018.1–1020.1 (22 specimens)

Order **Gleicheniales** Schimper 1869

Family **Matoniaceae** Presl 1847

Genus **Phlebopteris** Brongniart 1836

Phlebopteris angustiloba (Presl in von Sternberg) Hirmer and Hörhammer 1936

Figures 4f, g, 5a, b

Selected synonyms (for more details see Schenk 1867; Harris 1931).

- 1838 *Gutbiera angustiloba*—Presl in von Sternberg: p. 116, pl. 33, figs. 13a–e.
 1843 *Andriana baruthina*—Braun: p. 42, pl. 3–4, 6, 12, pl. 10, figs. 1–3.
 1867 *Gutbiera angustiloba* Presl—Schenk: p. 64, pl. 18, figs. 5–10.
 1867 *Andriana baruthina* Braun—Schenk: p. 87–89, pl. 21, figs. 1–7, pl. 22, fig. 1.
 1867 *Andriana baruthina* Braun—Schenk: p. 87, pl. 21, figs. 1–6.
 1891 *Laccopteris angustiloba* Presl—Raciborski: p. 15, pl. 2, figs. 6–9.
 1892 *Laccopteris angustiloba* Presl—Raciborski: pl. 2, fig. 22.
 1914 *Gutbiera angustiloba* Presl—Gothan: p. 99–100, pl. 17, fig. 5.
 1914 *Andriana baruthina* Braun—Gothan: p. 102, pl. 17, fig. 8, pl. 18, figs. 1–2.
 1914 *Andriana norimbergica*—Gothan: p. 102–103, pl. 17, figs. 6–7.
 1922 *Andriana baruthina* Braun—Krasser: p. 348.
 1931 *Laccopteris angustiloba* (Presl) Raciborski—Harris: p. 74–77, pl. 14, figs. 6–17, text-fig. 26.
 1936 *Phlebopteris angustiloba* (Presl)—Hirmer and Hörhammer: p. 26, pl. 6, text-fig. 5.3.
 1950 *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer—Lundblad: p. 23–24, pl. 2, fig. 14; pl. 3, figs. 1–5, pl. 13, fig. 2, text-fig. 4.
 ?1998 *Aninopteris formosa*—Givulescu et Popa: p. 52, pls. 1, 2, text-figs. 1–6.
 1993 *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer—Van Konijnenburg-van Cittert: p. 241–43, pl. 1, figs. 2, 5.
 1997 *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer—Popa: fig. 13.

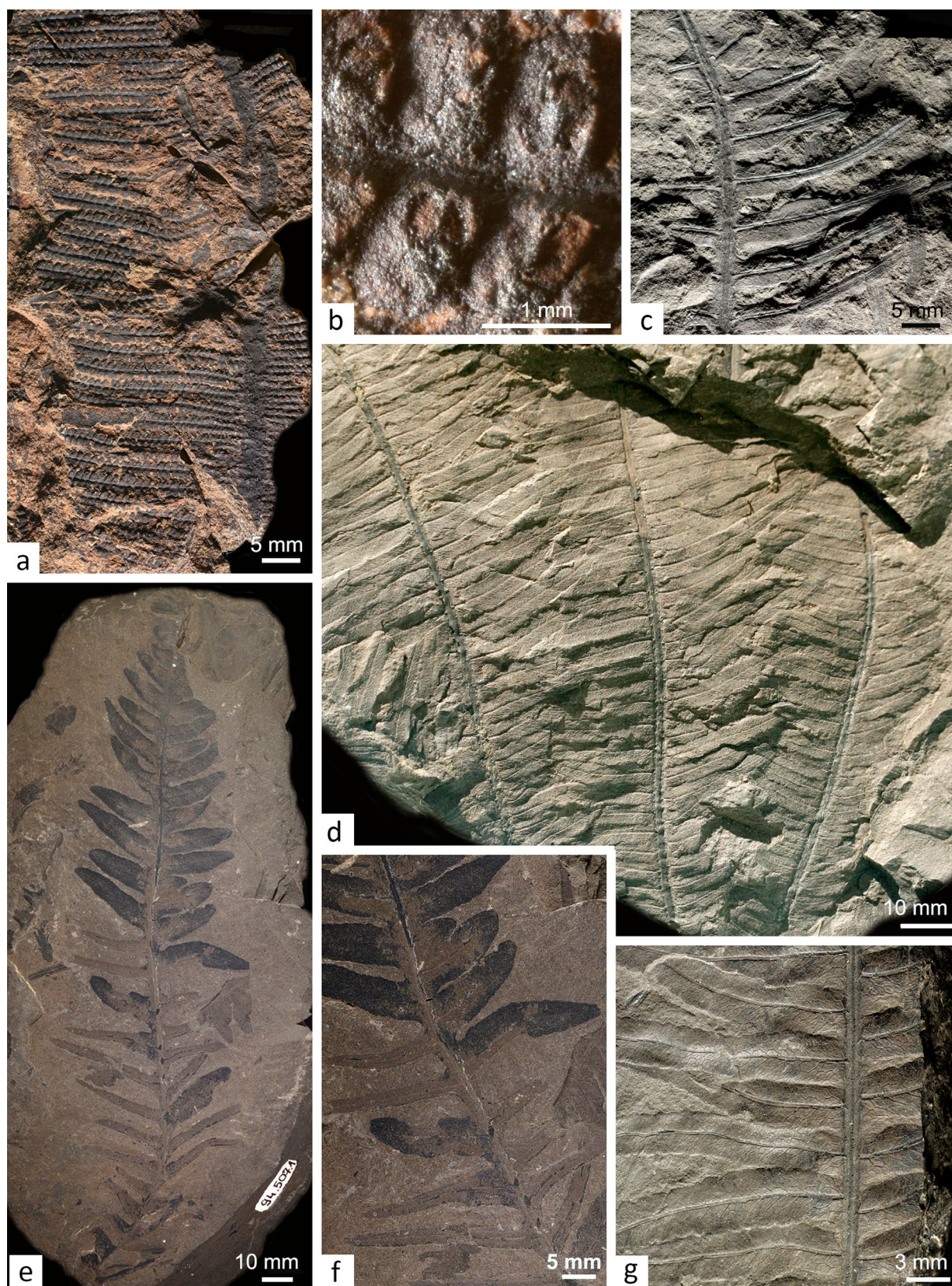


Fig. 5 Ferns of the Early Jurassic of Hungary. **a** *Phlebopteris angustiloba* (Presl in von Sternberg) Hirmer et Hörhammer 1936, pinna fragment, No. 89.485.1. (photo MS); **b** Detail of **a** with impressions of the sori (photo MS); **c** Pinnae with partly sterile and partly fertile pinnules of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., No. 2003.453.1. (photo MS); **d** Sterile frond fragment of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., holotype, No. 96.266.1.; **e** Pinnae with sterile and fertile pinnules of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., No. 94.507.1. (photo MS); **f** Detail of **e** of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov.; **g** Pinnae fragment with clear details of the pinnae attachment and venation pattern of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., No. 94.291.1. (photo MS)

- 2002 *Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer—Van Konijnenburg-van Cittert: p. 115, 119.
 ? 2002 *Phlebopteris muensteri* (Schenk) Hirmer et Hörhammer—Van Konijnenburg-van Cittert: p. 115.

Description. Fertile and sterile fronds are similar in gross morphology, palmately compound and slender. About 12 pinnae arise from the base, a petiole is not preserved (Fig. 4f). The rachis is 1–2 mm wide. The lamina of the attachment area of the pinnae is expanded (10 mm wide). Linear pinnules appear on the pinna rachis about 30–40 mm from the base; basal pinnules are short (20 mm long) and increase apically in size (up to 65 mm), while the width stays constant (2 mm). Pinnules are attached perpendicularly and with the entire width to the pinnae rachis; apical pinnules are inserted with an acute angle. Distance between basal pinnules is about 2 mm (rarely up to 4 mm), this distance decreases towards the apex, and pinnules may overlap almost over their entire length. The margin of the pinnules is entire, apex subacute. The lamina on both sides of the midrib is divided into almost square bulging units (about 0.7×1 mm) by secondary veins arising almost perpendicularly from the midrib (Fig. 4g). These veins branch on the bulging units nearly parallel to the midrib and subsequently 2–3 times diagonally across the units. Sori are attached on the fertile fronds within the units, in few remains of sporangia are preserved (0.3×0.5 mm, Fig. 5b).

Remarks. The Hungarian specimens are preserved mostly as small fragments, with the exception of one almost complete frond base, but the distinctive gross morphology (i.e. venation pattern) permits an attribution to *P. angustiloba*. Characteristic for this species is the presence of “rectangular units”. They are slightly convex on sterile fronds and distinctively convex on fertile fronds, indicating that the structure is independent from the presence of sori (Harris 1931). Schenk (1867, pl. 18, fig. 10) showed a similar venation pattern with only one bifurcation at half lamina and a second vein arising

from the base and extending up to the attachment of the sori at the middle part of the lamina.

In the past, sterile fragments were often attributed to the genus *Andriana* Braun 1840 (*A. baruthina* Braun 1840, *A. norimbergica* Gothan 1914), whereas fertile specimens were assigned to *G. angustiloba* Presl in Sternberg 1838. Krasser (1922), for example, mentioned *A. baruthina*, from the Mecsek Mts. but without description or illustration. Gothan (1914) distinguished the three fossil taxa mentioned before and excluded an affinity with the genus *Laccopteris* (junior synonym of *Phlebopteris*). Harris (1931) considered *G. angustiloba* and *A. baruthina* conspecific and moved them to *Laccopteris* (younger synonym of *Phlebopteris*). We agree with Harris and consider all three species conspecific and belonging to the genus *Phlebopteris*.

Each sorus of *P. angustiloba* consists of eight sporangia (Lundblad 1950). The in situ spores are generally trilete, sub-triangular (30–55 µm in diameter) with a distinct opening, interrachial thickenings and a smooth exine (e.g., Schenk 1867; Harris 1931; Reymanówna 1963; Van Konijnenburg-van Cittert 1993). The same spore type, belonging to the dispersed genus *Deltoidosporites* Danzè-Corsin and Lavein 1963, was described by Schenk (1867) for *A. baruthina*. Unfortunately, our material is too highly coalified for any sporangia details, but Götz et al. (2011) mentioned *Deltoidospora* for the Upper Triassic to Lower Jurassic sediments of Hungary.

Material. BP 89.96.1, 89.123.1, 89.192.1–193.1, 89.336.1, 89.339.1–440.1, 89.455.1, 89.482.1, 89.484.1–485.1, 89.488.1, 94.181.1, 94.454.1, 94.474.1–476.1, 94.482.1–483.1, 94.485.1, 94.509.1, 94.549.1, 94.601.1, 94.603.1, 94.642.1, 94.653.1–655.1, 94.681.1, 94.685.1, 94.725.1–726.1, 94.728.1, 94.791.1–793.1, 94.931.1, 96.121.1, 96.185.1, 98.791.1, 98.975.1, 2002.38.1 (42 specimens)

Phlebopteris kirchneri Barbacka and Kustatscher sp. nov.
 Figures 5c–g, 6a–g

Synonyms.

- 1961 *Phlebopteris muensteri* (Schenk) Hirmer et Hörhammer—Nagy: p. 618, pls. 8, 10.
 1961 *Phlebopteris* aff. *polypodioides* Brongniart—Nagy: p. 619, pl. 7, fig. 1.
 ? 1997 *Phlebopteris* sp. Kostina and Doludenko; p. 187, figs. 7b, 8k.

Etymology. In honor of Martin Kirchner who studied extensively the Rhaetian to Early Jurassic flora of Bayreuth (Germany).

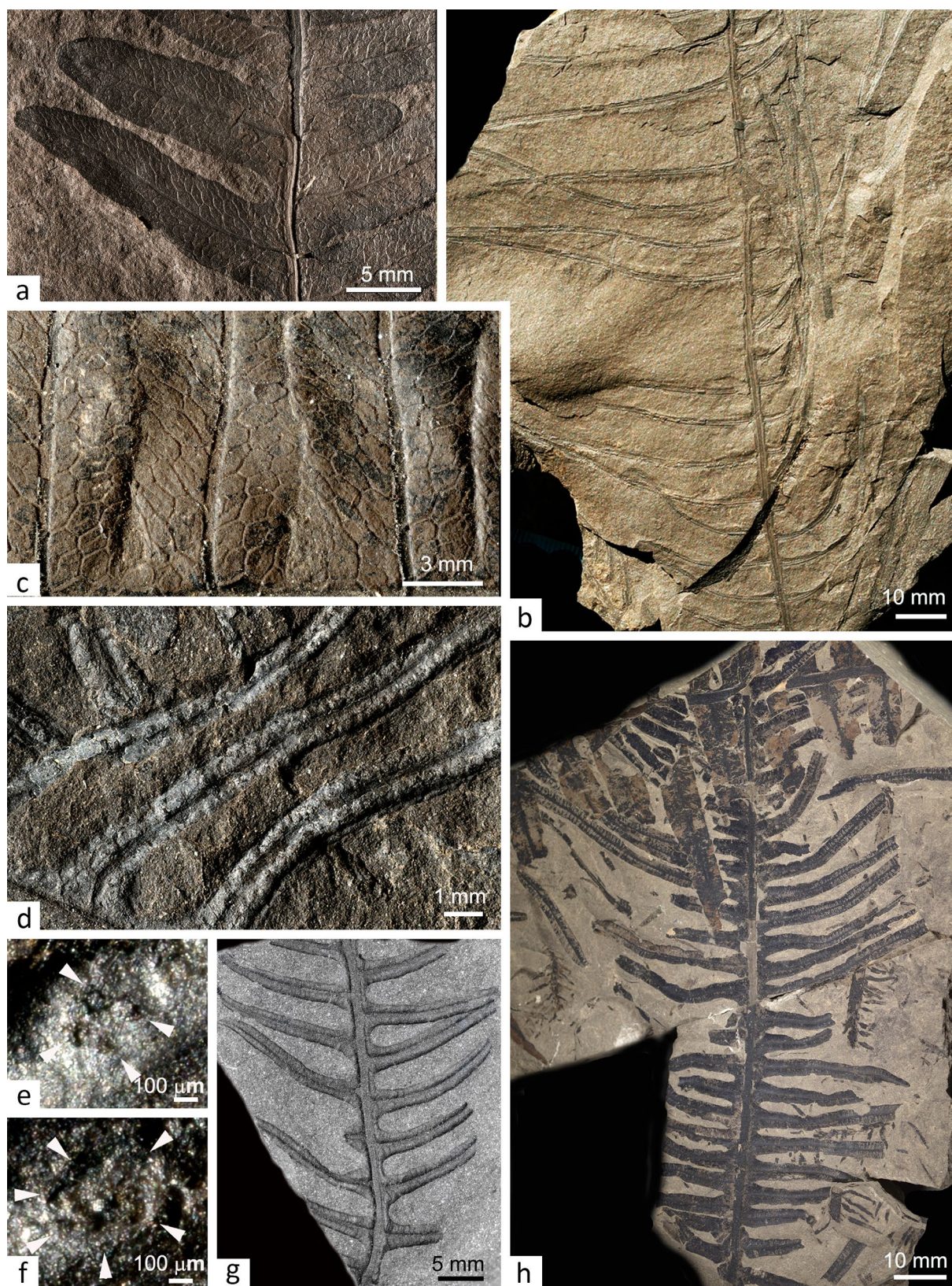


Fig. 6 Ferns of the Early Jurassic of Hungary. **a** Detail of sterile pinnules with clear venation pattern of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov. (photo MS); **b** fertile pinna fragment of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., paratype, No. 2004.69.1. **c** Detail of sterile pinnules with clear venation pattern of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., details of venation, No. 94.291.1. (photo MS); **d** detail of fertile pinnules with imprints of the sori of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., No. 2003.461.1. (photo MS); **e, f** details of Fig. 5d showing impressions of sporangia. (photo MS); **g** fertile pinna fragment of *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov., No. 94.522. (photo MS); **h** sterile pinna fragment of *Matonia braunii* (Goeppert) Harris 1980, No. 89.339.1. (photo MS)

Holotype. No 96.266.1. Hungarian Museum of Natural History, Fig. 5d, hic designatus.

Paratype. No 2004.69.1. Hungarian Museum of Natural History, Fig. 6b, hic designatus.

Type locality. Pécsbánya (near Pécs), Mecsek Mountains, Southern Hungary.

Locality and stratigraphic horizon. Pécsbánya (near Pécs), Mecsek Mountains, Southern Hungary, Mecsek Coal Formation, Hettangian, Early Jurassic.

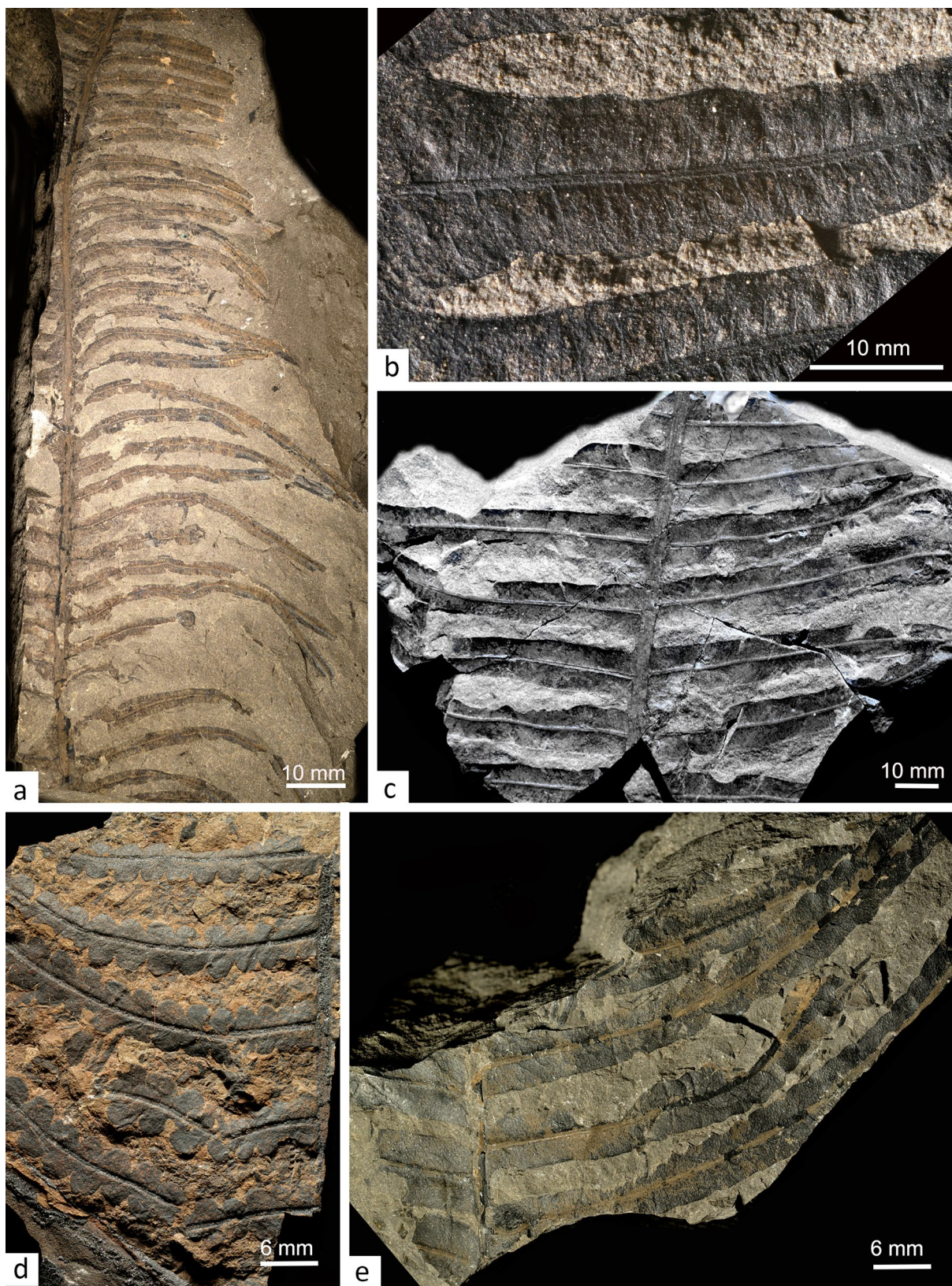
Repository. Botanical Department of the Hungarian Natural History Museum, Budapest

Diagnosis. Fronds palmate, large. Pinnae pinnate, free from the base, fertile fronds differ from sterile ones. Sterile pinnules linear, long, margins entire or slightly wavy, apex subacute. Pinnule bases as wide as the pinnule or slightly extended, touching, crowded, but not overlapping. Midrib conspicuous, secondary veins forming ovoid, rhomboid, or hexagonal meshes of almost equal size, running in two or three rows along the pinnule. Sterile and fertile pinnules mixed on the same pinnae, or on separate pinnae or separate fronds. Fertile pinnules narrow linear, widely spaced, or bases extended, in touch, apex subacute. Midrib distinct, secondary veins delicate. Round sori detached, densely inserted in single rows on both sides of the midrib, 5–6 sporangia each sorus.

Description. The fronds are palmate with more or less regular pinnae bases. The petiole is up to 7 mm wide and branches into 4–5 separate pinnae. Sterile and fertile pinnules are distributed mostly on distinct pinnae and fronds, but mixed pinnae and fronds have been observed as well (Fig. 5e, f). Occasionally, pinnules are basally sterile with a fertile apex (Fig. 5c). Sterile and fertile pinnules differ in shape and dimension. Pinnules are linear with an obtuse apex and a slightly extended (sometimes touching), rarely constricted base. Margins are almost parallel, entire or slightly

undulated. The midrib is distinct, secondary veins form a net of oval-rhomboid-hexagonal meshes of equal size, running in 2–3 rows along the midrib (Figs. 5g, 6c). Sterile pinnules are lanceolate (Fig. 5d). Basal pinnules are small (from 3 × 10 mm), but increase in dimension towards the middle part of pinna. They reach up to 85 mm in length and up to 5 mm in width. The distance between neighbouring pinnules is 1–3 mm. Fertile pinnules are narrower (2 mm, max 4 mm) and up to 90 mm long, the basal ones are ~ 15 mm long (Fig. 6b). They are widely spaced, with a distance of 3–18 mm. The midrib is distinct, but secondary veins are rarely visible. They form two rows of net meshes, where the second row may be incomplete with open meshes near the margin. Sori are always detached, only slight imprints are visible on the lower surface of the pinnules. They are round, about 1 mm in diameter with five to six (?) sporangia each (Fig. 6e, f). In situ spores are unknown.

Comparisons. *Phlebopteris kirchneri* Barbacka and Kustatscher sp. nov. differ from all other taxa because of its very regular venation pattern, consisting of the oval-to hexagonal meshes formed by secondary veins; shape, size and arrangement of the meshes are very constant in the specimens. In other species secondary veins near the midrib form relatively large, more or less prominent primary arches from which veins run towards the pinnule margin and anastomize, developing irregularly elongated meshes similar to *Phlebopteris polypodioides* Brongniart 1828, *P. woodwardii* Leckenby 1864 or *P. affinis* (Schenk) Seward 1900. Veins do not form meshes but are pinnate with a variable number of forking of the secondary veins in *P. dunkeri* Schenk 1871, *P. angustiloba*, *P. braunii* Göppert 1841 or *P. muensteri* (Schenk) Hirmer and Hörhammer 1936. Additionally, distinctive features are the distance between pinnules and the much narrower shape in fertile fronds. Fertile pinnules show a high variability in dimension and shape; this becomes visible because of the large number of studied sampled *P. kirchneri* Barbacka and Kustatscher sp. nov. resembles *P. tracyi* Ash 1991 from the Jurassic of Oregon and Idaho in general pinnule morphology and the reticulate pattern of the secondary veins at the pinnule margin. The basal (near the midrib) net venation is, however, more distinct and more regular in the new species. *Phlebopteris otongensis* Weber 2008 from the Jurassic of Mexico, has smaller linear to triangular pinnules (5.5 × 1.5 mm) and the crowded, sometimes anastomosing veins. In *P. muensteri* from the Early Jurassic of Europe and Asia the pinnules are larger (at least 60 × 4–5 mm), have a thick midrib and simple to twice forked lateral veins with a higher vein concentration (30–40 per cm). The pinnules are also bigger (80–150 × 10–14 mm) in *P. formosa* (Givulescu and Popa) Schweitzer et al. 2009 from the Early Jurassic of Romania. The lateral veins arise at 2–3 mm interval in the latter species, and bifurcate often giving origin to an almost



◀**Fig. 7** Ferns of the Early Jurassic of Hungary. **a** Fertile pinna fragment of *Matonia braunii* (Goeppert) Harris 1980, No. 89.336.1. (photo MS); **b** Sterile pinnules with venation pattern of *Matonia braunii* (Goeppert) Harris 1980, No. 89.339.1. (photo MS); **c** Sterile pinna fragment with entire margins of *Thaumatopteris brauniana* Popp 1863, No. 94.543.1; **d** Sterile pinna fragment with deeply incised margins of *Thaumatopteris brauniana* Popp 1863, No. 94.486.1. (photo MS); **e** Sterile pinna fragment with partly entire and partly incised margins of *Thaumatopteris brauniana* Popp 1863, No. 94.602.1. (photo MS)

fasciculate structure. Venations similar to those described here may also occur in *P. woodwardii* Leckenby 1864; however, the lamina of the latter species is very thick and generally preserved as fusain.

Remarks. This species is the most abundant among the ferns from Mecsek Mountains. The sterile and fertile frond fragments evidence a high variability in size and distance between single pinnules, especially in fertile ones. Venation pattern and frond shape, on the other hand, are consistent within the group. The specimens from the Mecsek Mts. described by Nagy (1961) as *P. muensteri* and *P. aff. polypodioides*, correspond to the sterile and fertile pinnae of *P. kirchneri* Barbacka and Kustatscher sp. nov., respectively; *P. muensteri* and *P. polypodioides* are not represented in this locality. *P. kirchneri* Barbacka and Kustatscher sp. nov. resembles also two specimens figured by Kostina and Doludenko (1997) from the Middle Jurassic of Siberia that show the same coarse reticulum as our specimens and could belong to the same species.

Material. BP 89.29.1, 89.300.1–302.1, 89.306.1–308.1, 89.335.1, 89.343.1, 89.345.1, 89.447.1, 89.465.1, 89.476.1, 89.478.1, 89.486.1, 89.489.1, 89.493.1, 89.495.2, 94.135.1, 94.248.1, 94.256.1, 94.291.1, 89.303.1, 94.312.1–313.1, 94.321.1, 94.333.1, 94.391.1–392.1, 94.472.1, 94.507.1, 94.522.1, 94.544.1, 94.566.1, 94.593.1, 94.658.1, 94.662.1, 94.729.1, 94.736.1, 94.784.1, 94.859.1, 94.862.1–863.1R, 94.996.1–998.1, 94.1000.1, 96.12.1–13.1, 96.134.1–135.1, 96.217.1, 96.230.1–232.1, 96.237.1–249.1, 96.256.1, 96.262.1–263.1, 96.266.1, 96.384.1, 96.387.1, 96.391.1, 98.53.1, 98.98.1, 98.178.1, 98.249.1, 98.341.1, 98.423.1, 98.584.1–595.1, 98.597.1, 98.713.1–714.1, 98.750.1, 98.778.1–792.1, 98.927.1, 98.1075.1, 98.1102.1, 2000.1282.1, 2000.1285.2, 2000.1287.1, 2001.625.1, 2001.979.1, 2002.4.1–15.1, 2002.17.1, 2002.19.1, 2002.25.1, 2003.190.1, 2003.446.1–457.1, 2003.461.1, 2003.471.1–473.1, 2004.61.1–78.1, 2004.1016.1, 2004.1090.1, 2004.1104.1–1111.1, 2004.1113.1, 2004.1184.1–1185.1, 2004.1199.1, 2005.639.1, 2005.642.1–643.1, 2005.885.1, 2005.890.1, 2005.949.1, 2005.959.1, 2006.680.1, 2006.682.1, 2006.684.1–2006.689.1, 2007.142.1, 2007.144.1–145.1, 2007.147.1,

2007.149.1–152.1, 2007.154.1, 2007.156.1, 2007.159.1, 2007.170.1–174.1, 2007.199.1, 2007.816.1, 2007.820.1, 2007.871.1, 2007.908.1. (172 specimens).

Genus *Matonia* R. Brown in Wallich 1830

Matonia braunii (Goeppert) Harris 1980

Figures 6h, 7a, b

Selected synonyms.

- 1980 *Matonia braunii* (Goeppert)—Harris: p. 296–300, text figs. 1–20.
- 1997 *Matonia braunii* (Goeppert) Harris—Papa: fig. 19.
- 1999 *Matonia braunii* (Goeppert) Harris—Van Konijnenburg-van Cittert and Morgans: p. 47, pl. 2, fig. 4, text fig. 21C.
- 2016 *Matonia braunii* (Goeppert) Harris—Barbacka et al.; p. 860, figs. 2–5.

Description. The frond is palmately compound with pinnate pinnae. The fertile and sterile frond fragments were not found in anatomical connection, but share the same gross morphology. Both sterile and fertile pinnules are oppositely to suboppositely insert on the rachis. The lamina of neighbouring pinnules joins at the base, forming an about 1 mm wide, U-shaped web along the rachis. The biggest sterile pinnule fragment is 57 mm long (with an estimated length of 70 mm), the longest fertile pinnule is more than 80 mm (incomplete). The width of both pinnule types is similar (3 mm) and both narrow before the subacute apex. The distinct midrib runs up to the apex. Secondary veins are delicate, arise nearly perpendicularly to the midrib and fork once, usually close to the margin (Fig. 7b). They form rectangular, slightly bulging units clearer visible in the fertile pinnules. Sori are poorly and only sporadically preserved, with up to six sporangia. Fragments of annuli are present, but badly preserved; indusia are not observed.

Remarks. The fern remains show clear similarities with *P. braunii* Göppert 1841 including the pinnae size, pinnule shape and arrangement, venation pattern and sori. Harris (1980) considered the sterile fronds *P. braunii* and the fertile fronds *P. muensterii* Schenk 1867 as belonging to the same natural species and attributed them to the genus *Matonia* due to the presence of indusia characteristic for this genus. He considered specimens without indusia as having lost them, similar to extant Matoniaceae in which indusia detach very easily. This was confirmed by the discovery of *M. braunii* fronds with indusia in Lower Jurassic sediments of Poland (Barbacka et al. 2016). Although venation was poorly preserved in the Polish specimens, its pattern and

Table 1 Occurrence of fern taxa in the other localities over the world (Presl in von Sternberg 1820–1838; De Zigno 1856–68; Lindley and Hutton 1831–37; Schenk 1867; Schimper 1869; Nathorst 1878; Raciborski 1890, 1894; Zeiller 1903; Seward 1911; Halle 1913; Gothan 1914; Antevs 1919; Krasser 1922; Johansson 1922; Thomas 1922; Oishi 1939–40; Kawasaki 1939; Harris 1931, 1961; Lundblad 1950; Kimura 1959; Daber 1962; Kilpper 1964; Weber 1968; Tralau 1965; Herbst 1971; Schweitzer 1978; van der Burgh and van Konijnenburg-van Cittert 1984; Gee 1989; Givulescu and Popa 1989; Van Konijnenburg-van Cittert and van der Burg 1989; Ash 1991; Dobruskina 1994; Kostina and Doludenko 1997; Popa 1997; Wang 2002; Van Konijnenburg-van Cittert 2002; Barbacka and Bodor 2008; Bodor and Barbacka 2008; Barbacka et al. 2010; Bomfleur and Kerp 2010; Kiritchkova and Nosova 2011; Jarzynka 2016)

Taxon	Green-land	Arctic Archipelago	Europe										Asia							South Hemisphere	
			Eng-land	Scot-land	France	Ger-many	Swe-den	Aus-tria	Italy	Hun-gary	Roma-nia	Poland	Russia	Iran	Afghani-stan	Viet-nam	Korea	China	Japan	Argen-tina	Antarc-tica
<i>Marattiopsis hoerensis</i>			x				x			x											
<i>Todites princeps</i>	x		x			x				x		x		x	?	x		x	x		
<i>Todites goeppertianus</i>	x					x		x		x									x		
<i>Cladophlebis denticulata</i>	x		x	x		x		x		x		x		x				x	x	x	x
<i>Cladophlebis haiburnensis</i>			x							x	x	x	x	x			x		x		
<i>Cladophlebis roessertii</i>	x				x	x	x			x		x	x	x		x		x	x		x
<i>Phlebopteris angustiloba</i>	x	x				x	x	x		x		x							x		
<i>Phlebopteris kirchnerii</i>										x			?								
<i>Matonia braunii</i>	x		x							x		x									
<i>Thaumatopteris brauni-ana</i>	x		x			x	x	x		x		x		x	x						

Table 1 (continued)

Taxon	Green-land	Arctic Archipelago	Europe				Asia										South Hemisphere				
			Eng-land	Scot-land	France	Ger-many	Swe-den	Aus-tria	Italy	Hun-gary	Roma-nia	Poland	Russia	Iran	Afghani-stan	Viet-nam	Korea	China	Japan	Argen-tina	Antarctica
<i>Clathropteris meniscoides</i>		x				x	x			x	x						x		x		x
<i>Dictyophyllum nilssonii</i>	x					x	x	x		x								x			
<i>Dictyophyllum rugosum</i>							x														

other morphological features correspond with our remains from Hungary even if in our case indusia were not found. This species is well known from the Jurassic of Greenland and Europe (Table 1).

Material. BP 89.123.1, 89.336.1, 89.339.1, 89.488.1, 89.488.1R, 94.601.1, 94.603.1, 94.642.1, 94.791.1, 94.931.1 (10 specimens)

Family **Dipteridaceae** Seward and Dale 1901

Genus *Thaumatopteris* Göppert 1841

Thaumatopteris brauniana Popp 1863

Figures 7c–e, 8a

Selected synonyms (for more details see Schenk 1867; Harris 1931, Schweitzer 1978).

- 1863 *Thaumatopteris brauniana*—Popp: p. 409.
- 1867 *Thaumatopteris brauniana* Popp—Schenk: p. 73–75, pl. 18, figs. 1–3, pl. 19, fig. 1.
- 1878 *Thaumatopteris schenkii*—Nathorst: p. 46, pl. 2, fig. 1.
- 1914 *Thaumatopteris schenkii* Nathorst—Gothan: p. 104–5, pl. 19, figs. 3, 3a.
- 1922 *Thaumatopteris brauniana* Popp emend. Nathorst—Krasser: p. 351.
- 1922 *Thaumatopteris schenkii* Nathorst—Krasser: p. 353.
- 1931 *Thaumatopteris schenkii* Nathorst—Harris: p. 93–94, pl. 17, figs. 6–8, pl. 18, figs. 1–2, text-fig. 35.
- 1931 *Thaumatopteris brauniana* Popp—Harris: p. 94–96, pl. 17, figs. 5, pl. 18, figs. 4, 6–11, 13, text-fig. 36.
- 1950 *Thaumatopteris brauniana* Popp—Lundblad: p. 27, pl. 4, figs. 1–2.
- 1950 *Thaumatopteris schenkii* Nathorst—Lundblad: p. 28, pl. 3, figs. 10–11, pl. 4, fig. 1.
- 1961 *Thaumatopteris schenki* Nathorst—Nagy: p. 622, pl. 11, fig. 2.
- 1978 *Thaumatopteris brauniana* Popp—Schweitzer: p. 36, pl. 4, figs. 5–9, pl. 5, figs. 1–7, pl. 6, figs. 1–3; text-figs. 20, 23, 24, 26–28, 30–31.
- 1997 *Thaumatopteris* sp.—Popp: figs. 8–11.
- 2003 *Thaumatopteris brauniana* (Popp) Schweitzer—Popp et al.: p. 362–364, pl. 1, figs. 1–5,

Description. Fronds are palmate, with fertile and sterile fronds similar in morphology. From each basal branch a maximum of seven pinnae arise. Pinnae are linear to lanceolate; the fragments reach a maximal length of 250 mm, but the shape permits a much higher estimation for the total length. The longest pinnules are in the middle part of the pinna, with decreasing length towards base and apex. The

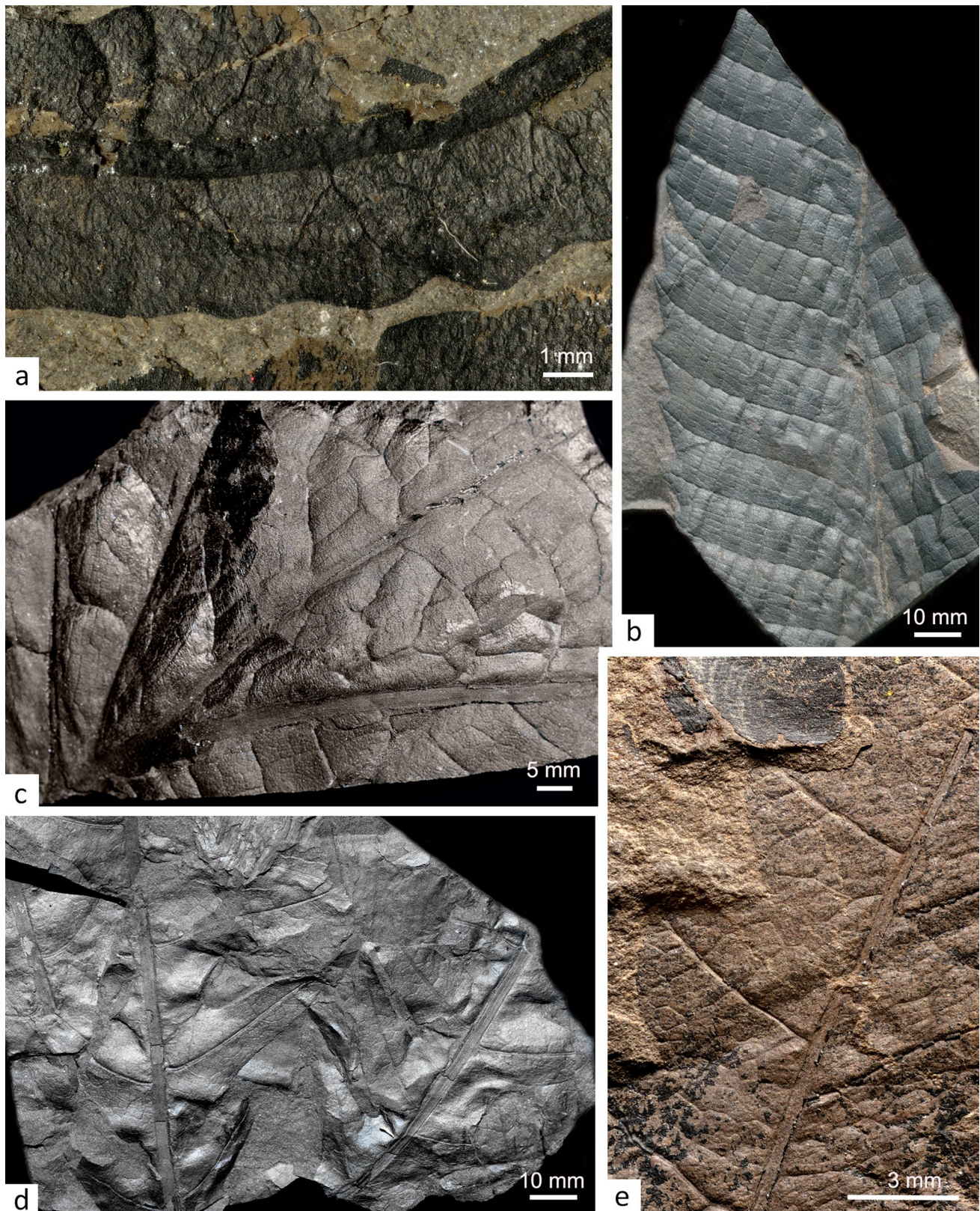


Fig. 8 Ferns of the Early Jurassic of Hungary. **a** *Thaumatopteris brauniana* Popp 1863, sterile pinnules with venation pattern, details from Fig. 7f. (photo MS). **b** Pinna fragment of *Clathropteris meniscoides* Brongniart 1835–36, No. 98.342.1. **c** Base of frond of *Clath-*

ropteris meniscoides Brongniart 1835–36, No. 89.315.1. **d** Frond fragment of *Dictyophyllum nilssonii* (Brongniart) Goeppert 1846, No. 96.78.1. **e** Frond fragment of *Dictyophyllum nilssonii* (Brongniart) Goeppert 1846, No. 96.221.1 (photo MS)

rachis is 1.5–4 mm wide and slightly striated. Pinnules arise perpendicularly from the rachis, with a usual distance between adjacent pinnules of 3 mm (max. 10 mm). Pinnule bases range from slightly constricted to slightly extended. Pinnules are elongate with a subacute apex, up to 10 mm long and 10 mm wide at the pinna base, increasing to more than 130 mm (incomplete) in length, and up to 13 mm in width in the middle. The pinnule margin is often entire (Fig. 7c), though it may be waved to deeply incised (reaching the midrib, Fig. 7d). The ratio of fragments with entire margins to those with incised margins is 5:1. Frequently, the margin is entire in the basal portion and becomes waved or incised towards the apex (Fig. 7e). The midrib is distinct, secondary veins divide once near the midrib and form a net of delicate veins with nearly hexagonal meshes (the smallest meshes are 0.3 mm wide, Fig. 8a). Sori are globose with a diameter of 0.8–1 mm, but fertile specimens are poorly preserved.

Remarks. The Hungarian frond fragments show a high variability in size and margin of the pinnules. Forms with different margins were originally distinct in separate fossil species, e.g., *Thaumatopteris schenki* Nathorst 1878 with incised margins, *T. brauniana* Popp 1863 with entire margins, *T. variabilis* Stanislawski 1976 with partly entire and partly incised pinnules and *T. bipinnata* Kilpper 1964 with deeply incised margins giving almost the idea of a bipinnate structure. Schweitzer (1978) interpreted the different pinnule forms as a result of natural leaf variability and included the above mentioned species in *T. brauniana* according to its nomenclatural priority. Moreover, Schweitzer et al. (2009) suggested that there was no fundamental difference in leaf morphology between *Thaumatopteris* and *Dictyophyllum*. Harris (1931) and Schweitzer et al. (2009) proposed to distinguish between the two genera based on the sori position, dimension and number of sporangia, and in case those are missing, to treat the specimens as *Dictyophyllum*. Since the type species of *Thaumatopteris*, *T. muensteri* Göppert, 1841 has been moved by Nathorst (1875) to *Dictyophyllum*, the genus *Thaumatopteris* is now without type species. The currently best defined fossil taxon of *Thaumatopteris* is *T. brauniana* (Schweitzer et al. 2009) but the genus will need to be conserved (pers. Comm. van Konijnenburg-van Cittert 2018). Krasser (1922) and Nagy (1961) mentioned *T. schenki* and *T. brauniana* from the Mecsek Mts, but we follow Schweitzer (1978) using the name *T. brauniana*.

Material. BP 89.332.1, 89.338.1, 89.343.1R, 89.347.1, 89.458.1, 89.466.1–467.1, 89.469.1–471.1, 89.473.1, 89.483.1, 89.488.1, 89.494.1, 94.175.1, 94.231.1, 94.441.1, 94.448.1–449.1, 94.467.1, 94.486.1–489.1, 94.498.1, 94.508.1, 94.531.1, 94.543.1, 94.545.1–547.1, 94.554.1, 94.593.1, 94.601.1–602.1, 94.605.1–607.1, 94.652.1,

94.690.1, 94.695.1, 94.725.1, 94.730.1, 94.767.1, 94.794.1–795.1, 94.822.1, 94.825.1–826.1, 94.828.1, 94.830.1–831.1, 94.860.1–863.1, 96.129.1–131.1, 96.136.1, 96.146.1, 96.175.1, 96.223.1, 96.383.1–384.1, 96.403.1, 98.582.1, 2004.73.2, 2004.1113.1 (53 specimens)

Genus *Clathropteris* Brongniart 1828

Clathropteris meniscoides Brongniart 1835–36

Figure 8b, c

Selected synonyms (for more details see Schenk 1867; Johansson 1922; Harris 1931).

- 1825 *Filicites meniscoides*—Brongniart: p. 200, pls. 11–12.
- 1828 *Clathropteris meniscoides*—Brongniart: p. 62, 194.
- 1841 *Clathropteris platyphylla*—Göppert: pl. 18, 19, figs. 1–3.
- 1867 *Clathropteris platyphylla* Brongniart—Schenk: p. 81–86, pl. 16, figs. 2–9, pl. 27.
- 1914 *Clathropteris platyphylla* Göppert—Gothan: p. 107.
- 1922 *Clathropteris meniscoides* Brongniart—Johansson: p. 10, pl. 4, fig. 13, pl. 5, figs. 53–56.
- 1931 *Clathropteris meniscoides* Brongniart—Harris: p. 88–93, pl. 15, figs. 1, 9, pl. 16, figs. 9–10, pl. 13, figs. 3, 5, 12, text-figs. 32–34.
- 1939–40 *Clathropteris meniscoides* Brongniart—Oishi: p. 214–16, pl. 3, figs. 1, 1a.
- 1989 *Clathropteris meniscoides* Brongniart—Givulescu: p. 19.
- 2002 *Clathropteris meniscoides* Brongniart—Van Konijnenburg-van Cittert: p. 120.

Description. The frond is large, palmate with long pinnae. The only petiole preserved is 16 mm wide and divides apically into two short branches from which originate at least four pinnae. The lamina of all pinnae is fused at their base over a distance of several centimetres giving origin to a solid fan-shaped basis. The largest preserved base fragment is 25 cm long with four pinna bases fused over a distance of more than 20 cm. The pinnae are elongated truncate, sometimes linear with an enlarged base and a subacute apex. The pinna width varies depending on the size of the frond and its position on the frond. The narrowest pinna fragment is 20 mm wide (apical?), the broadest (middle part?) 90 mm. Margins are waved to serrate, teeth vary in size within one pinna, up to a maximum of 5 mm. Midrib is marked, 1–4 mm wide, and extending up to the apex. Secondary veins form distinct polygons, each divided by meshes of fine tertiary veins. The meshes of the secondary veins are

irregular in shape and size at the base of the lamina, but rectangular, from 5×2 mm to 14×6 mm, in the pinna. No fertile fronds were observed, despite the large number of specimens.

Remarks. According to several authors (e.g., Harris 1931; Johansson 1922) *C. meniscoides* and *C. platyphylla* Göppert 1841 are conspecific with *C. meniscoides* having priority. *C. lunzensis* Stur 1881 differs from *C. meniscoides* in its larger marginal teeth (Harris 1931). The specimens from the Mecsek Mts. show a high variability in gross-morphology and pinnae shape and venation but fall within the species variability of *C. meniscoides*. Krasser (1922), Nagy (1961) and Van Konijnenburg-van Cittert (2002) considered it a common fern in the Jurassic flora of Hungary.

Material. BP 60.158.1, 89.41.1–45.1, 89.47.1–64.1, 89.66.1, 89.69.1, 89.76.1–77.1, 89.79.1–81.1, 89.84.1, 89.87.1, 89.90.1–91.1, 89.94.1, 89.98.1, 89.101.1, 89.112.1, 89.114.1–116.1, 89.118.1, 89.120.1–122.1, 89.124.1, 89.126.1, 89.134.1, 89.137.1, 89.141.1–144.1, 89.171.1, 89.314.1–316.1, 89.324.1, 89.326.1, 89.333.1, 89.340.1, 89.342.1, 94.76.1, 94.267.1, 94.332.1, 94.337.1, 94.472.1–473.1, 94.508.1, 94.561.1–573.1, 94.577.1–591.1, 94.729.1–730.1, 94.733.1, 94.736.1, 94.740.1, 96.137.1, 96.451.1, 98.270.1, 98.709.1–98.715.1, 2001.967.1, 2004.1112.1, 2005.648.1, 2005.900.1, 2005.941.1, 2007.138.1, 2007.145.1, 2007.147.1–150.1, 2007.157.1–159.1, 2007.176.1–184.1, 2007.896.1, 2007.954.1, 2009.467.1 (147 specimens)

Genus *Dictyophyllum* Lindley and Hutton 1834

Dictyophyllum nilssonii (Brongniart) Goeppert 1846
Figure 8d, e

Selected synonyms (for more details see Harris 1931).

- 1836 *Phlebopteris nilssoni*—Brongniart: p. 376, pl. 132, fig. 2.
- 1846 *Dictyophyllum nilssoni* Brongniart—Goeppert: p. 119.
- 1922 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Krasser: p. 350.
- 1831 *Dictyophyllum nilssonii* (Brongniart)—Goeppert: p. 81–85, pl. 14, fig. 4, pl. 15, figs. 3, 5, 6, 8, pl. 16, figs. 1–5, 7, 8, pl. 17, fig. 9, text-figs. 29–30.
- 1939–40 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Oishi: p. 218–9.
- 1962 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Daber: p. 131–132, pl. 4, fig. 7.

- 1968 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Weber: p. 49–50, pl. 8, figs. 67–72.
- 1997 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Popa: figs. 1–4.
- 2002 *Dictyophyllum nilssonii* (Brongniart) Goeppert—Wang: p. 130, 133.

Description. The species is represented in the flora only by sterile frond fragments. The fronds are palmate with up to 12 pinnae arising from a 10–20 mm wide petiole. Pinnae are lanceolate, 20–45 mm wide with a midrib of 1–4 mm width. The pinna margin is lobed with more or less deep incisions. Basally, below the first lobes, and near the apex the lamina is entire, 20–30 mm wide with slightly waved margins. Lobes start 30–40 mm from the base of the pinnae. They have a wide base, but radically narrow towards the apex which is usually obtuse. Lobes along the pinnae vary in form and size, from narrow (30×5–6 mm) to wide (50×13–25 mm) and are acroscopically enlarged. The margins of lobes are entire to slightly waving. The main vein of the lobes arises from the midrib and runs up to the tip of the lobes. Secondary veins form rounded, polygonal to irregular meshes.

Remarks. The flora of Hungary yielded so far only sterile frond fragments. Harris (1931) described different pinnae of *D. nilssonii* with transitional forms from Greenland, that convinced him to consider some earlier species, such as *D. spectabilis* Nathorst 1906, *D. nilssonii* var. *hoerense* Nathorst 1906, *Dictyophyllum acutilobum* (Braun) Schenk 1867 p.p. and *D. obtusilobum* Schenk 1867 p.p., as synonyms of *D. nilssonii*. The main criteria to distinguish the species, according to Harris (1931), are frond size, pinnae morphology (length and lobation) and features of sporangia. Sterile and fertile fronds have a similar morphology, although large fronds are more often fertile. Sporangia are scattered and do not form sori; they are attached above small veins in the meshes (Harris 1931). Harris (1931) used the terms “pinnules” for lobes and “rachis” for the midrib of the pinna. Since the lobes in fact do not correspond to separated pinnules, we prefer to use lobes as proposed by Seward (1911).

Dictyophyllum nilssonii differs from all other species because of its robust fronds, generally wide and short lobes and sporangia size. However, marginal lobes in the pinnae may be confusing, since very long lobes may have lobed margins (e.g., *Dictyophyllum rugosum* or large forms of *D. nilssonii*; Harris 1931), resembling *Thaumatopteris braunii*. In the Mecsek Mts. *D. nilssonii* is common and its frond show a high variability in size and shape of the lobes.

Material. BP 89.10.1, 89.12.1, 89.28.1, 89.67.1, 89.70.1, 89.89.1, 89.440.1, 89.455.1–456.1, 89.459.1–461.1,

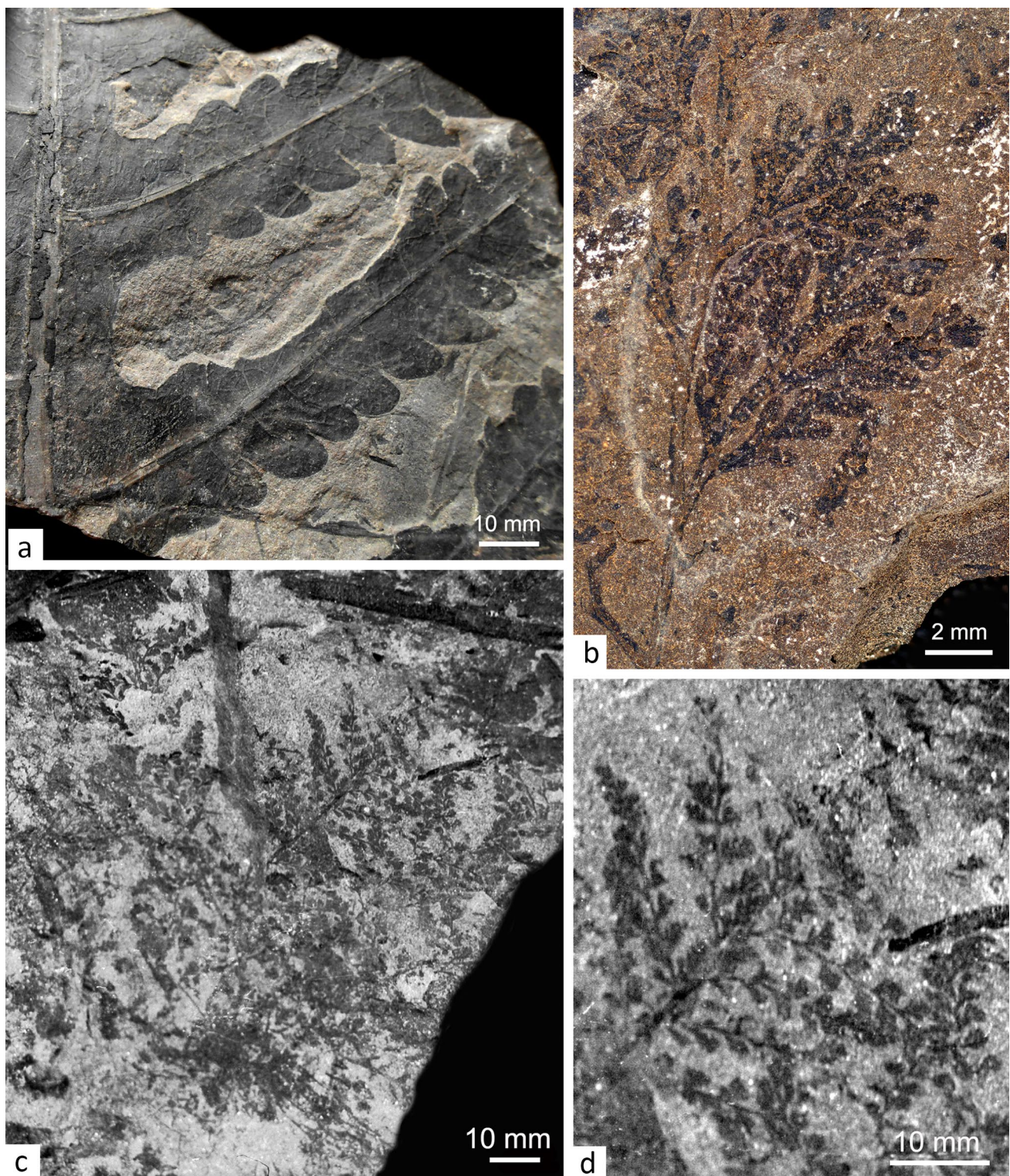


Fig. 9 Ferns of the Early Jurassic of Hungary. **a** Pinna fragment of *Dictyophyllum rugosum* Lindley and Hutton 1834 emend. Harris 1961, No. 59.267.1., Komló. **b** Pinna fragment of *Coniopteris* sp.,

No. 2001.626.1. (photo MS). **c** The lost juvenile plant of *Coniopteris* sp. with fragment of rhizome and roots, archive photo. **d** Detail from **c**

89.463.1, 89.465.1–466.1, 89.482.1–483.1, 94.136.1–138.1, 94.231.1, 94.267.1, 94.338.1–339.1, 94.342.1, 94.344.1, 94.397.1, 94.424.1, 94.424.1R, 94.439.1, 94.476.1, 94.487.1, 94.509.1–510.1, 94.549.1–550.1, 94.554.1, 94.663.1, 96.57.1, 96.78.1–81.1, 96.83.1–89.1, 96.132.1, 96.171.1, 96.181.1–184.1, 96.360.1–367.1, 96.480.1, 98.345.1, 98.348.1, 2000.1159.1, 2002.4.1, 2002.136.1 (72 specimens).

Dictyophyllum rugosum Lindley and Hutton 1834 emend. Harris 1961
Figure 9a

Selected synonyms (for more details see Harris 1961).

- 1834 *Dictyophyllum rugosum*—Lindley and Hutton: p. 65, pl. 104.
- 1856–68 *Dictyophyllum rugosum* Lindley et Hutton—De Zigno: p. 176–178, pl. 23, figs. 1–2.
- 1867 *Dictyophyllum acutilobum*—Schenk: p. 77, pl. 19, figs. 3–5, pl. 20, fig. 1.
- 1922 *Dictyophyllum rugosum* Lindley et Hutton—Hamshaw: p. 110–116, figs. 1–5.
- 1961 *Dictyophyllum rugosum* Lindley et Hutton—Harris: p. 176–178, pl. 23, figs. 1–2.
- 1961 *Thaumatopteris muensteri* (Göppert) Nathorst—Nagy: p. 621, pl. 11, fig. 1.
- 1961 *Thaumatopteris muensteri* Göppert var. *longissima* Schenk—Nagy: p. 621, pl. 13, fig. 3.
- 1961 *Dictyophyllum acutilobum* (Braun) Schenk—Nagy: p. 622.
- 2002 *Dictyophyllum rugosum* Lindley et Hutton—Wang: p. 130, 133, pl. 4, figs. 1–4.
- 2011 *Dictyophyllum rugosum* Lindley et Hutton—Kiritchkova and Nosova: p. 55, pl. 4, figs. 4–6, pl. 5, fig. 1.

Description. The frond fragments are sterile, preserved as separated lobes, only in few specimens the rachis is preserved. The basal part of the fronds is not preserved. The rachis is up to 5 mm wide. The lobes are 75–85 mm long and 8–20 mm wide (max. 30 mm). They are widely spaced and have almost parallel (or slightly tapering), waved to lobed margins. Secondary lobes may be deeply incised (3–5 mm), sometimes even teeth-shaped; their apex is obtuse to subacute. The midrib is distinct, secondary veins form dense irregular, reticulate meshes.

Remarks. *Dictyophyllum rugosum* differs from *D. nilssonii* in having longer and deeper (sometimes double) lobed pinnae with more delicate veins. Two specimens with strongly developed teeth-shaped lobes resemble *D. acutilobum* (Braun) Schenk 1867, a younger synonym of *D. nilssonii*

(Harris 1931). We attribute the specimens from Mecsek to *D. rugosum* because of the double lobation (*D. nilssonii* is never double lobed) and the secondary lobes which are exceptionally regular with acute apices. The specimens attributed by Nagy (1961) to *D. acutilobum*, *T. muensteri* (Göppert) Nathorst 1956 and *T. muensteri* var. *longissimi* Schenk 1867, after re-examination are included into *D. rugosum*.

Harris (1961) described fertile frond fragments of this species with sessile sporangia (which may form sori of 1–4 sporangia). The in situ spores (~40 µm diameter) are tetrahedral with thick, smooth walls, a distinct trilete mark with a distinct laesura of the dispersed *Deltoidosporites* type of spore. Götz et al. (2011) mentioned *Deltoidospora* for Upper Triassic–Lower Jurassic sediments of Hungary.

Material. BP 89.458.1, 89.465.1, 89.488.1, 94.168.1, 94.273.1, 94.281.1, 94.283.1, 94.335.1–336.1, 94.377.1, 94.380.1, 94.383.1, 94.402.1, 94.410.1, 94.412.1–413.1, 94.415.1–416.1, 94.004.1, 94.426.1, 94.429.1, 94.431.1, 94.434.1, 94.436.1, 94.824.1, 94.827.1, 94.829.1, 94.883.1, 96.57.1, 96.69.1, 96.74.1, 96.82.1, 96.185.1, 96.221.1, 96.346.1, 98.791.1, 2002.32.1, 2002.137.1, 2003.464.1, 2004.60.1, 2005.823.1 (41 specimens).

Order **Cyatheaales** Frank in Leunis 1877
Family **Dicksoniaceae** Schomb. 1848

Genus **Coniopteris** Brongniart 1848

Coniopteris sp.
Figure 9b–d

Description. The most complete fossil corresponds to a juvenile? plant with a rounded rhizome fragment and thin roots (less than 1 mm wide). The sterile fronds are bipinnate, up to 80 mm long and 30 mm wide. The rachis is 0.5 mm wide, with 8–20 mm long and up to 5 mm wide pinnae. Pinnules are slightly catadromic, 2–4 mm long, and 0.5–2.5 mm wide. They are more or less deeply dissected with 3–5 lobes. The apheleiform pinnules are found at the pinna bases. Fertile fronds are not preserved.

Remarks. The genus *Coniopteris* is common in the Jurassic of the Northern Hemisphere, although it is more frequent in the Middle Jurassic. Harris (1961) described six species of *Coniopteris* from the Middle Jurassic of Yorkshire which differ in shape of pinnules and form of fertile fronds. The specimens from the Mecsek Mts. resemble *Coniopteris hymenophylloides* (Brongniart) Seward 1900 emend. Harris, 1961, because pinnae and pinnules do not overlap and the pinnules are slightly catadromic. The apheleiform pinnules situated basiscopically are also a typical feature

of this species (Van Konijnenburg-van Cittert and Morgans 1999). The specimens have also some features of *C. murrayana* (Brongniart) Brongniart emend. Harris 1961 like tapering pinnae and delicate pinnule shape. According to Harris (1961) the fronds of *C. murrayana* are much larger than those of *C. hymenophylloides*, but in Hungarian material the frond size remains unresolved since the most complete specimen corresponds probably to a juvenile plant. The pinnule shape resembles some sterile pinnules of *C. margaretae* Harris 1961, widely represented in Middle Caspian Basin (Kiritchkova and Nosova 2011), but margins of *C. margaretae* are more deeply and irregularly incised. As a whole plant our specimen resembles *Coniopteris braunii* Brongniart 1828 as illustrated by Schenk (1867, pl. 6, figs. 6, 7), which shows similar juvenile fronds.

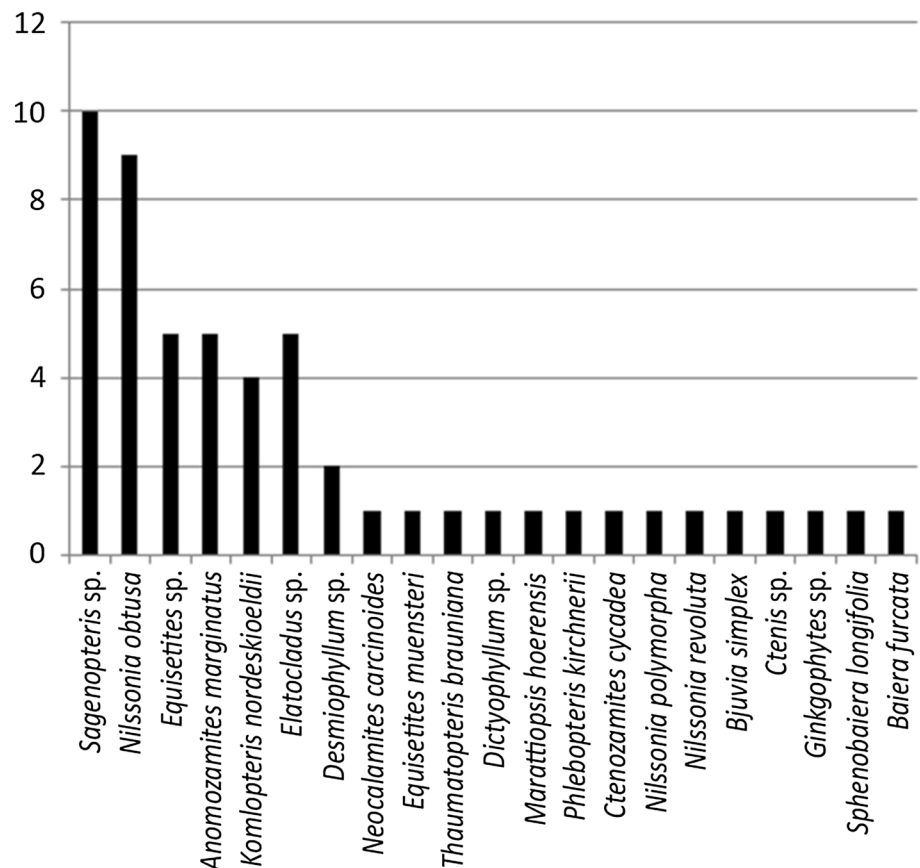
Götz et al. (2012) evidenced *Cyathidites minor* Couper 1958 and *Concavisporites parvulus* sensu Bona 1995 as dispersed Dicksoniaceae spores in the Upper Triassic–Lower Jurassic of Hungary. Van Konijnenburg-van Cittert (1989) described in situ spores of six *Coniopteris* species as trilete, subtriangular to triangular in shape, in some species with a margo, in others with a perispore. This would correspond both to the dispersed *Concavisporites* Pflug in Thomas and Pflug 1953 and *Cyathidites* Couper 1953 genera.

Material. The described specimen, unfortunately, belonged to a private collection and was lost; only pictures confirm this record. The Hungarian Natural History Museum holds two other specimens which are small fragments of poorly preserved pinnae: BP 2001.626.1, 2001.627.1.

Discussion

All fern species represented in the Lower Jurassic sediments of the Mecsek Mountains (Hungary) are widely known from numerous localities of the Northern Hemisphere (Table 1). Most are typical elements of Lower Jurassic floras, with the exception of *Coniopteris* sp., which was more common during the Middle Jurassic. In the Mecsek Mts. their richness is expressed both in a high abundance and species diversity. They are often preserved in fine-grained sediments which permitted a good preservation of the morphology of the fronds, even if the material was highly coalified, impeding the preservation of in situ spores. The high number of fertile and sterile fronds permits proving high intraspecific variability in some taxa. Some species described by Nagy (1961) from the study locality are revised in this paper. This concerns specimens attributed by that author to *P. braunii* that are now included in *C. denticulata*, and *Phlebopteris* aff. *polypodioides*, ascribed in this paper to *M. braunii*.

Fig. 10 Number of fern taxa co-occurring with other plant species



Specimens assigned previously to *Dictyophyllum acutiloba*, *T. muensteri* and *T. muensteri* var. *longissima* were moved to *D. rugosum*. Frond fragments described as *P. muensteri* (Nagy 1961) have been attributed to a new species, *P. kirchneri* n.sp. *Selenocarpus* sp., mentioned by Nagy (1961), cannot be revised due to the lack of specimens or any other data like illustration or description.

The Hungarian Jurassic fern assemblage is composed of Marattiaceae (*Marattiopsis*, one species), Osmundaceae (*Todites*, *Cladophlebis*, five species), Matoniaceae (*Phlebopteris*, *Matonia*, three species), Dipteridaceae (*Thaumatopteris*, *Clathropteris*, *Dictyophyllum*, four species) and Dicksoniaceae (*Coniopteris*, one species). Quantitatively, the most common genera are *Phlebopteris* (214 specimens), *Clathropteris* (147 specimens), and *Cladophlebis* (121 specimens), followed by *Dictyophyllum* (113 specimens), *Todites* (99 specimens), *Thaumatopteris* (53 specimens), *Marattiopsis* (46 specimens), *Matonia* (10 specimens) and *Coniopteris* (three specimens). At family level, the Dipteridaceae (313 specimens) would thus be the most abundant group, followed by Matoniaceae (224 specimens) and Osmundaceae

(220 specimens), whereas Marattiaceae (46 specimens) and Dicksoniaceae (three specimens) are rare.

Co-occurrences of the different fern taxa

Although ferns are abundant and most diverse in the Jurassic of the Mecsek Mts., their co-occurrence with other plants is relatively low. Out of 49 plant fossil taxa only 21 are associated with at least one fern fragment. Among 35 non-fern taxa, seven co-occur with at least two fern species (Fig. 10). A maximum co-occurrence has been observed for *Sagenopteris* sp., which co-occurs with 10 different fern species, and *Nilssonsonia obtusa*, associated with nine species. *Equisetites* sp., *Anomozamites marginatus* and *Elatocladus* sp. co-occur with five species each, *Komlopteris nordeskoeldii* with four species and *Desmiophyllum* sp. with two species. Associated with one fern taxon only are the seed fern *Ctenozamites cycadea*, the cycads *Nilssonsonia polymorpha*, *Nilssonsonia revoluta*, *Bjuvia simplex*,

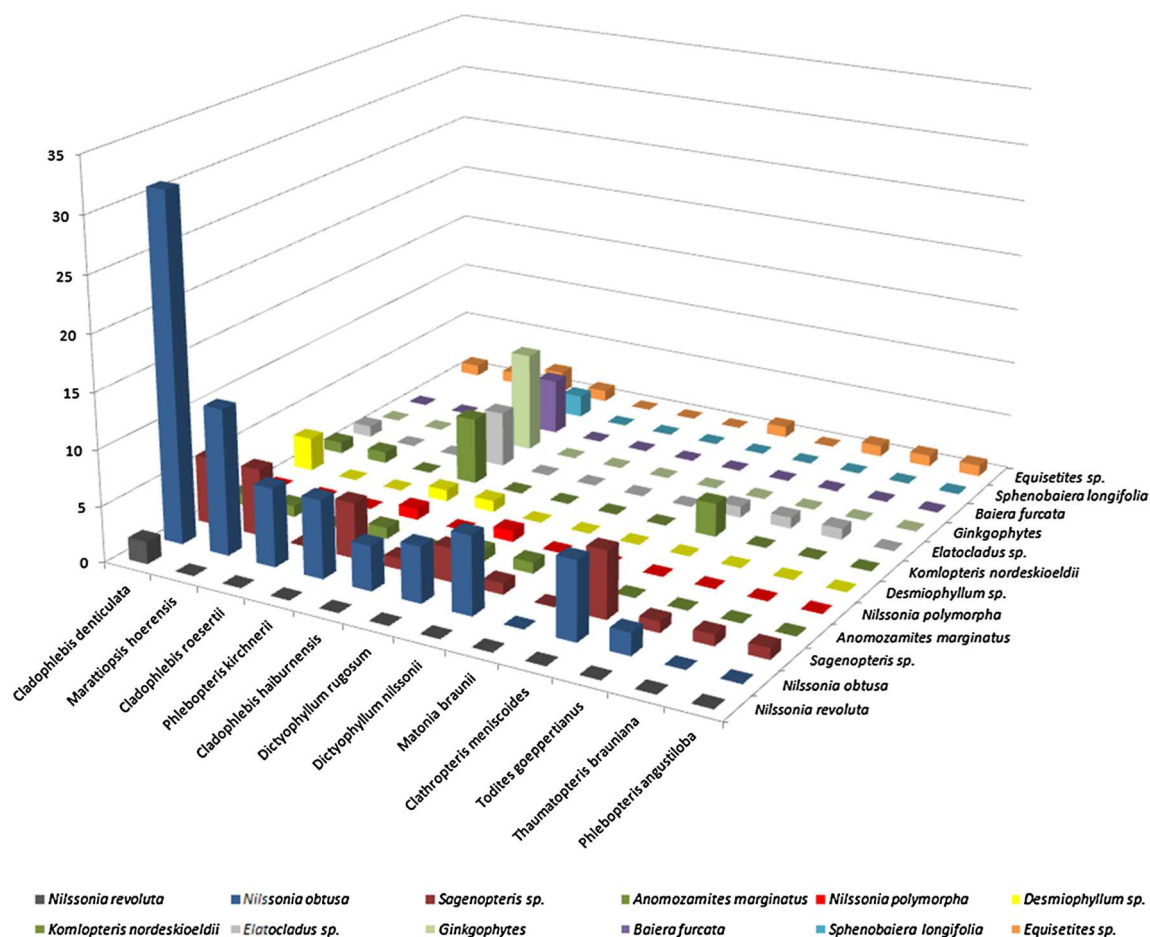
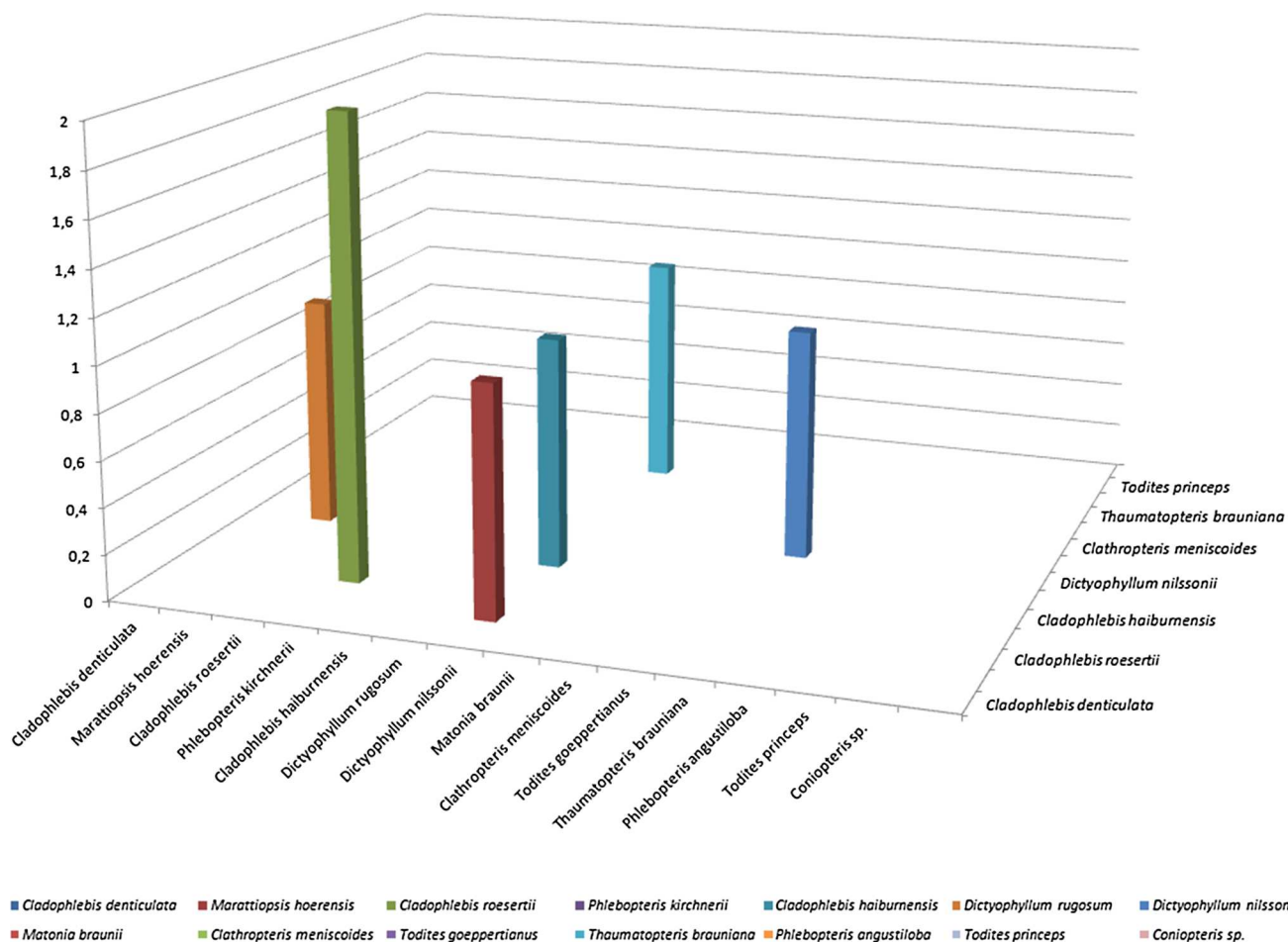
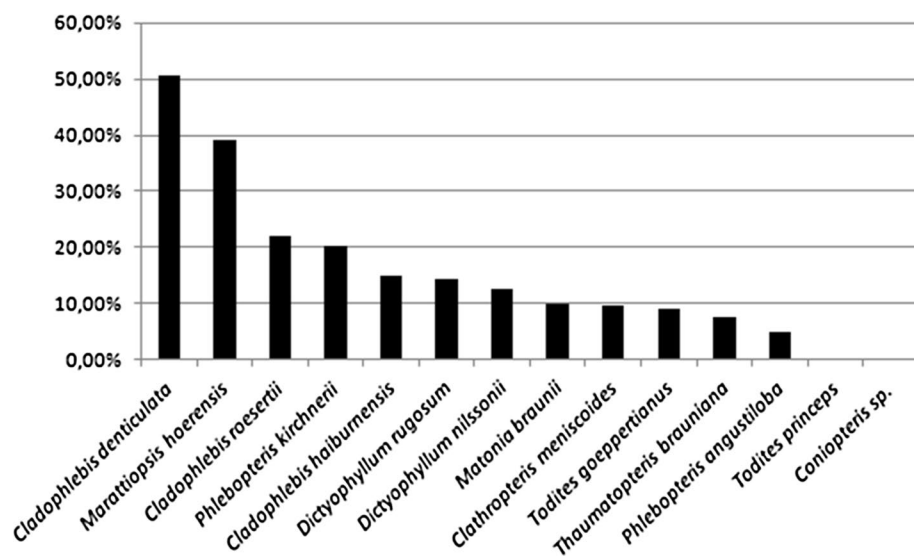


Fig. 11 Co-occurrence of ferns with other plant taxa

Fig. 12 Percentage of co-occurring fern species**Fig. 13** Co-occurrence between different fern taxa

Ctenis sp. and the ginkgophytes *Sphenobaiera longifolia* and *Baiera furcata*.

Nilssonia obtusa has quantitatively the most co-occurrences with ferns and its frequency is highest with *C. denticulata* (31 specimens) and *M. hoerensis* (13 specimens). The remaining specimens co-occur fewer than ten times (four in seven specimens, three in six, once five, once four and once two specimens, the rest are associated with single specimens). A relatively high co-occurrence is observed between *P. kirchneri* and the ginkgophytes (16 specimens with indet. ginkgophytes, *B. furcata* and *S. longifolia*). This fern species is actually the only one associated with ginkgophyte leaves (Fig. 11).

All ferns show significant disproportion between quantity of co-occurring and not co-occurring samples. The most frequently co-occurring fern species is *C. denticulata* with almost 50% specimens associated with other plant remains (Fig. 12). *M. hoerensis* co-occurs for 40% and *C. roessertii* and *P. kirchneri* for 20%, *C. haiburnensis*, *D. rugosum* and *D. nilssonii* less than 15%, *M. braunii*, *C. meniscoides*, *T. brauniana* are associated for less than 10% of their specimens, *P. angustiloba* for less than 5%. Two taxa are not associated with any other remains, *Coniopteris* sp. and *T. princeps*, but the former is represented only by three specimens. Seven (out of 14) fern taxa are associated with other fern remains (four pairs); the resulting pairs are *C. roessertii* and *P. kirchneri*, *C. haiburnensis* and *D. nilssonii*, *D. nilssonii* and *T. brauniana*, as well as *D. rugosum* and *M. hoerensis*.

However, often only single specimens of each species are associated; even the very abundant *P. kirchneri* (associated with 13 different taxa) is associated with *C. roessertii* on two samples only (Fig. 13).

PCA and cluster analyses

In earlier published statistical analyses carried out on the entire plant assemblage from the Jurassic of the Mecsek Mts., five eco-groups were distinguished (Barbacka 2011) based on the species co-occurrence on the same specimens and sedimentological data. The identified environments were influenced mostly by disturbance and water availability and included (1) moderately disturbed, relatively drier inland areas (*Sagenopteris* ecogroup); (2) highly disturbed short-lived, moderately wet territories of alluvial deposits (*Thaumatopteris* ecogroup); (3) moderately disturbed swamps (*Komlopteris* ecogroup); (4) weakly disturbed, moderately wet canopy (*Ptilozamites* group) and (5) weakly disturbed wetlands (*Ginkgoites* ecogroup). Not all fern taxa were used in this analysis. Among the excluded taxa were *C. meniscoides*, *T. princeps*, *T. goeppertianus* and *C. roessertii* because of their low co-occurrence and low abundance in relation to the other flora elements. *M. braunii* was not identified at that time and *P. kirchneri* appeared as *Phlebopteris* sp. Accordingly to the previous study (Barbacka 2011) most ferns had their maximum occurrence in disturbed and

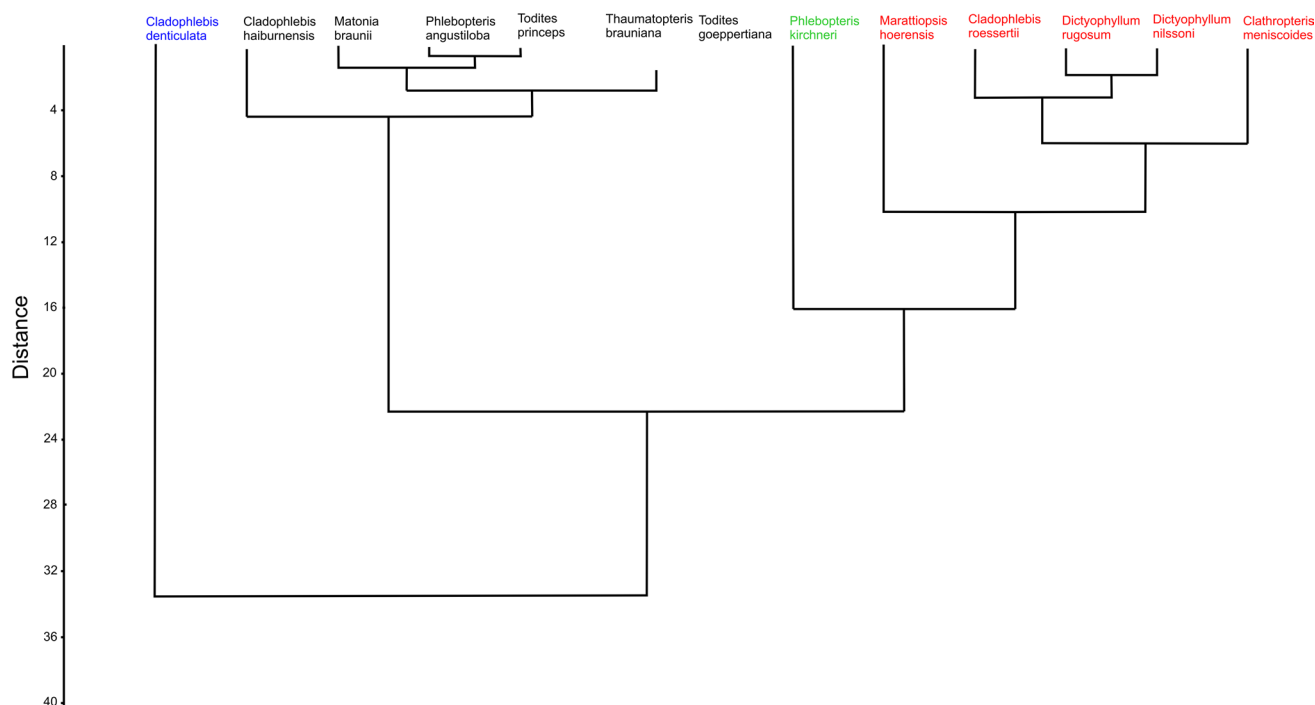


Fig. 14 Dendrogram result of Ward cluster analyses. The different colours represent the different eco-groups of ferns

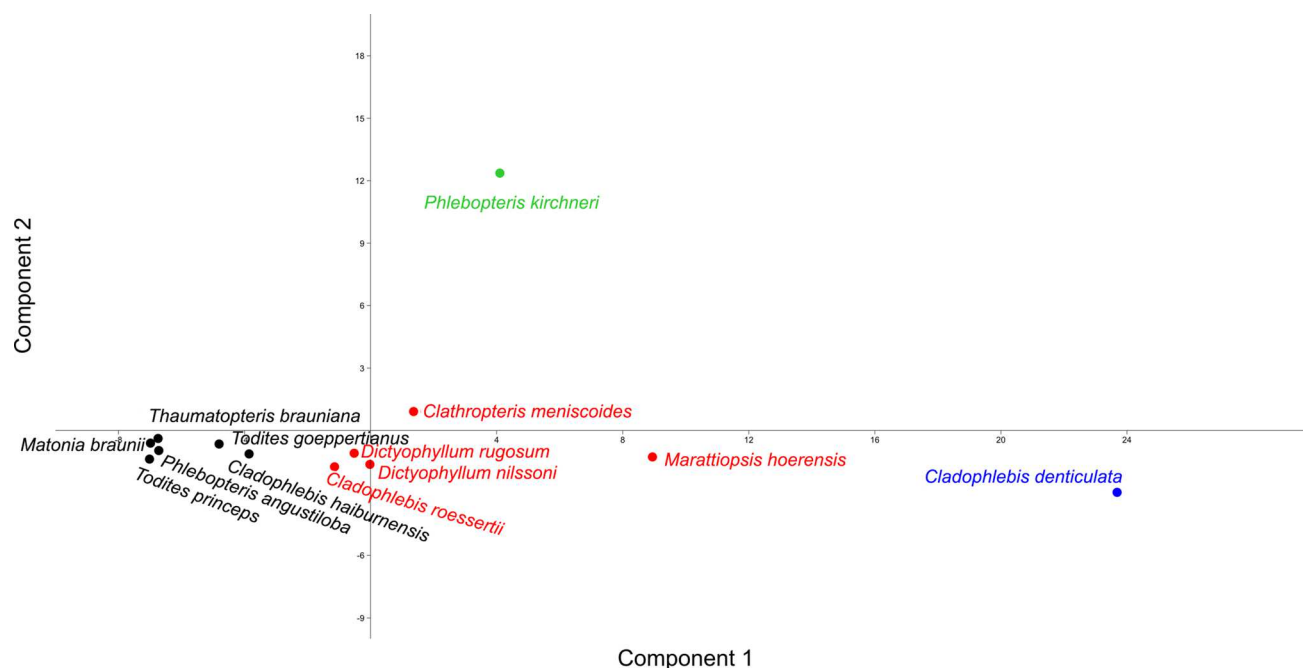
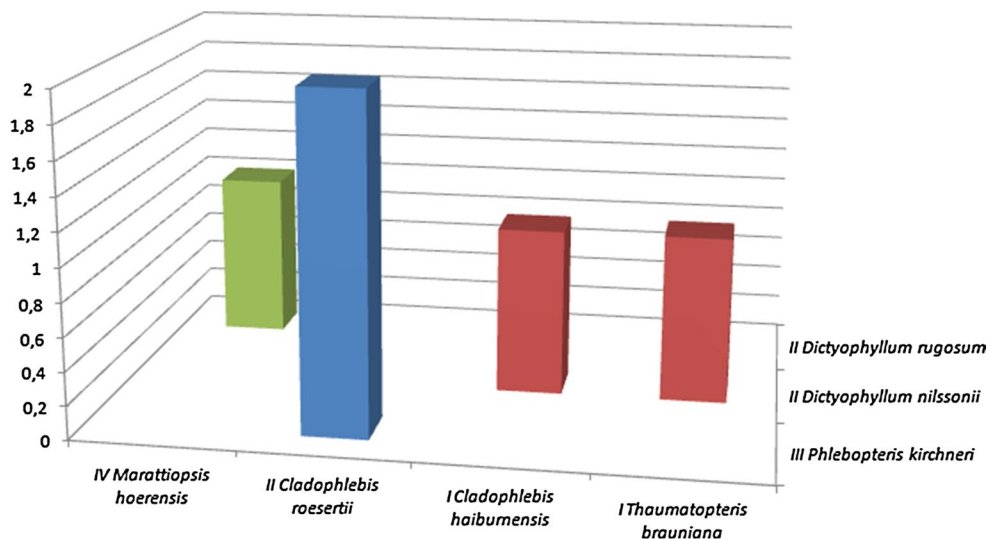


Fig. 15 Visualisation of the first two components of PCA analyses. Colours symbolize the eco-groups formed by cluster analyses

rather wet environments (*Thaumatopteris* ecogroup was represented exclusively by ferns and horsetails), whereas some were connected with drier, and moderately to less disturbed habitats. No fern taxon has its maximum appearance in the wettest, swampy environment (*Komlopteris* ecogroup) including most of ginkgophytes, although *P. kirchneri* co-occurs with all types of ginkgophyte remains. The present statistical analysis with special focus on the ferns improves considerably the insight on their interaction, and includes all fern taxa with the exception of *Coniopteris* sp. because of too low number of specimens.

The cluster analysis based on the co-occurrence of ferns with all other taxa from the locality separates four major fern groups (Fig. 14). Fern species were differentiated the same way using PCA (Figs. 15, S3). The first group includes *T. goeppertianus*, *T. brauniana*, *T. princeps*, *P. angustiloba*, *M. braunii* and *C. haiburnensis*. The second group encloses *D. nilssonii*, *D. rugosum*, *C. roessertii*, *C. meniscoides* and *M. hoerensis*. Both groups are situated in the field 3 of the PCA plot, and close along component 1, excluding *C. meniscoides* which is placed in field 2, thus showing slight opposition along component 1 and *M. hoerensis* located in the field

Fig. 16 Distribution of co-occurring fern taxa in the ecogroups



4, showing a positive trend along component 1. The third group is monospecific with *P. kirchneri* and occupies the field 2, having positive values in component 2. *C. denticulata* forms the fourth group, also monospecific, located in field 4, and spreads to the positive values of component 1. It is apparent that the groups show a significant dispersion over the plot, reflecting their different requirements/adaptations. For interpretation we used the same environmental factors that were concluded for the whole flora from the Mecsek Mts. (Barbacka 2011), thus the component 1 reflects a wetter (left) to drier (right) environment and component 2 disturbed (bottom) to undisturbed (top) conditions, this attributes most ferns to rather wet and disturbed environment (field 3). In this case, *C. denticulata* would grow in the most dry, and *P. kirchneri* in the less disturbed habitat. Most taxa are influenced by component 1, suggesting that moisture is the decisive factor in fern ecological requirements. This is evident by the fact that PC1 explains 79% of the total variance while PC2 explains 15%. The groups 1, 2 and 4 are influenced in the same degree by disturbance, but are spread along moisture gradient.

Regarding the co-occurrences, the first group represents taxa co-occurring in the lowest degree, while taxa spread along the first two components (*P. kirchneri*, *C. denticulata* and *M. hoerensis*) are the most associated with other plants. It is noteworthy that the groups do not form common assemblages and are not attributed to a certain type of environment, but to a certain set of environmental conditions. Taxa in the same groups are not necessarily growing together. In fact, the co-occurring fern taxa belong to different PCA groups (see Fig. 16), which means that they could meet on the boundaries of their ecological ranges. The Ward cluster analysis reflects the groups from the PCA, but here *P. kirchneri* is close to the second group indicating that the cluster analysis does not detect disturbance as a significant factor.

Suggested environmental requirements of the ferns

Ecological considerations on fossil ferns are mostly based on comparisons with extant representatives, since only few in situ findings exist to date. Extant Marattiaceae are arborescent plants with large fronds that live under warm and moist circumstances such as understorey in forests. In the Jurassic of Yorkshire, fossil forms occur mainly in floodplain deposits, whereas a tree-fern habit was never demonstrated (Van Konijnenburg-van Cittert 2002). However, our studies suggest for the only marattialean fern taxon of the Hungarian Jurassic, *M. hoerensis*, drier environments than for most ferns, because of its frequent co-occurrence with *N. obtusa* and *Sagenopteris* sp. (see also Barbacka 2011).

Osmundaceae (*Cladophlebis* and *Todites*) are known as small arborescent plants with slender stems (Schenk 1867; Schweitzer 1978; Taylor et al. 2009; Pole 2014) preferring warm and humid environments, such as riverbanks, lake shores, fresh-water marshes, or brackish-water environment near the sea coast (Harris 1961; Vakhrameev 1991; Van Konijnenburg-van Cittert and Van der Burg 1996; Deng 2002; Wang 2002; Van Konijnenburg-van Cittert 2002; Sun et al. 2010). *C. denticulata* was the most important fern in coal layers in Romania. It colonized areas in the closing stages of the mire development together with *T. brauniana* and *D. nilssonii* or formed monospecific assemblages (Van Konijnenburg-van Cittert 2002; Popa 1997, 1998, 2000, 2014; Popa and Meller 2009; Barbacka 2011; Barbacka et al. 2015, 2016). However, the Hungarian plant remains were found in all rock types except channel fill deposits, indicating that the habitat of *C. denticulata* extended towards dry and moderately disturbed conditions with a high environmental tolerance (Barbacka and Bodor 2008; Barbacka 2011; Bodor and Barbacka 2012). *C. roessertii*, on the other hand, shows preferences directed towards slightly wetter conditions. Unfortunately, the low number of specimens preserved does not indicate any clear association with other plants apart from *P. kirchneri* and *N. obtusa*. Nonetheless it could have been part of diverse vegetation as suggested for other floras (Harris 1926; Gee 1989).

Cladophlebis haiburnensis and *T. goeppertianus* lived probably in slightly more disturbed and wetter environments than *C. roessertii*, probably alluvial deposits (islands, forelands), periodically damaged by floodings and occupied by colonizing plants (Barbacka 2011). *C. haiburnensis* was found in foliated siltstones attributed to lake or swamp deposits, whereas *T. goeppertianus* was found on a wide range of rock types indicating a high environmental adaptation for this species (Barbacka 2011; Bodor and Barbacka 2012). *T. princeps* occupied, according to the PCA plot, the wettest habitats in Mecsek (Bodor and Barbacka 2012). *T. princeps* occurred in the Early Jurassic of China and Poland in humid habitats surrounding lakes and rivers (Wang 2002; Wang et al. 2005; Barbacka et al. 2010). Harris (1961) suggested for *T. princeps* an epiphytic lifestyle, other authors (Schenk 1867; Weber 1968; Batten 1974; Schweitzer 1978; Hesselbo et al. 2003; Barbacka 2011) reconstructed it with quickly growing rhizomes and with short stems (max 30 cm) colonizing muddy soils due to the finding of short in situ stems in growth position with attached fronds.

The ecology of the matoniacean ferns during the Mesozoic is variable. Matoniaceae are known as arborescent ferns (Wang 2002) although some fossil taxa such as *P. polypodioides* and *Matonia pectinata* were reconstructed with short stems and an extended rhizome system (Schweitzer 1978). *P. kirchneri*, *P. angustiloba* and *M. braunii* from Mecsek could have a similar morphology. Ferns with rather large fronds,

such as *P. angustiloba*, could have grown under humid conditions in the understorey or as pioneer plants of disturbed, short-lived, moderately wet areas formed by alluvial deposits (Barbacka 2011). Other matonialean ferns were more stress-adapted (Van Konijnenburg-van Cittert, 2002). *P. kirchneri* is the fern with the widest spectrum of co-occurring plants, both in number of taxa and number of occurrences. Barbacka (2011) attributed it (mentioned as *Phlebopteris* sp.) due to its large fronds and thin lamina to the undisturbed, moderately wet canopy. On our PCA plot, this species stands out in environmental preferences, being highly tolerant with one of the widest environmental distributions among the ferns (Barbacka 2011). *M. braunii* occurs in the Early Jurassic of Poland in situ in a flood-plain-backswamp environment at the transition zone between floodplain (crevasse splay-delta) and lacustrine-back-swamp zones (Barbacka et al. 2016). On the PCA plot this species evidences the same requirements as *T. princeps*, in the wettest places grown by ferns.

Dipteridaceae during the Mesozoic occupied mainly humid and temperate-warm to subtropical climate zones. They are considered opportunistic plants colonizing disturbed habitats such as stream sites, riverbanks, exposed ridges and clearings (Cantrill 1995; Van Konijnenburg-van Cittert 2002; Bomfleur and Kerp 2010). The genera *Clathropteris*, *Dictyophyllum* and *Thaumatopteris* are considered herbaceous plants (Schweitzer 1978; Wang 2002; Bomfleur and Kerp 2010). Wang (2002) suggested *Dictyophyllum* with large fronds to be a dweller of humid environments and low light conditions (understorey). *D. nilssonii* and *D. rugosum* lay in the PCA plot close together in habitats with reduced humidity and with a low degree of disturbance, similar to most ferns. However, the co-occurring *N. obtusa*, *Sagenopteris* sp. and *A. marginatus* are connected to more stabile environments. Barbacka (2011) attributed *D. rugosum* to the highly disturbed and moderately wet areas formed by alluvial deposits, whereas *D. nilssonii* was part of the weakly disturbed canopy together with *P. kirchneri*. *T. brauniana* has been reconstructed with several metres long horizontally growing rhizomes (Schweitzer 1978) due to its resemblance with *Dipteris* Reinwardt, 1825. Barbacka (2011) considered this species a colonizer plant of highly disturbed and moderately wet habitats. However our analysis places this species in the wettest and most disturbed habitat similar to *T. princeps* and *M. braunii*. *C. meniscoides* was reconstructed in Antarctica as herbaceous understory in open vegetation dominated by bennettitaleans that became a dominant element during the colonization phase of disturbed sites after catastrophic volcanic events (Bomfleur and Kerp 2010). This species was also considered forming large monotypic thickets in disturbed environment in Early Jurassic of Patagonia, as a colonizing plant (Choo et al. 2016). In Hungary *C. meniscoides* occurs with *N. obtusa*, *K. nordeskioldii*,

Sagenopteris sp., *Elatocladus* sp. and *Equisetites* sp. and is close to both *Dictyophyllum* species on the PCA plot.

Extant Dicksoniaceae are tree-ferns in tropical and temperate rain forests, preferring thus warm and humid habitats (Vakhrameev 1991; Van Konijnenburg-van Cittert 2002). Most Mesozoic dicksoniaceous ferns are herbaceous with creeping rhizomes and grew in warm and humid climate zones of the Northern Hemisphere (Europe and Asia; Sun 1986; Deng 1995; Deng and Chen 2001). During the Lower Jurassic the dicksoniaceous ferns, such as *Coniopteris*, were rather small plants colonizing the margins of swamps (Wang 2002; Deng and Lu 2006).

Concluding remarks

Ferns are the most diverse group in the Mecsek Mts., both considering their number (more than 800 samples; about 16% of total number of collected material) and diversity (14 out of 55 taxa). Five families were recognized so far from the locality including Dipteridaceae (48% of the collected ferns), Matoniaceae (25%), Osmundaceae (21%), Marattiaceae (6%) and Dicksoniaceae (three specimens). Most taxa are attributed to relatively wet (non swampy) and disturbed habitats, but *C. denticulata* shows significant tendency to drier conditions and *P. kirchneri* sp. nov. to more stabil environment with better This was interpreted as growing in extended arborescent to herbaceous monospecific thickets in areas threatened by flooding along channels and river banks.

The Early Jurassic sediments of the Mecsek Mts. locality represent delta plain environment with a slow transition from delta to lake and lake-lagoonal environment in combination with fluctuations of the sea level due to several transgressions and regressions. The territory was rich in water, with peat-forming marshes along the river branches or lakes (Van Konijnenburg-van Cittert 2002; Barbacka and Bodor 2008; Barbacka 2011; Götz et al. 2011). The climate was humid and warm (Nagy and Nagy 1969; Paál-Solt 1969; Némédi Varga 1995, 1998; Barbacka 2011). The low degree of fragmentation and the very good preservation in most plant remains suggest a (par-)autochthonous deposition of the plant remains.

The ferns occupied more or less wet territories in this generally humid delta plain, although not all taxa were peat-forming and restricted to such environments (e.g., Van Konijnenburg-van Cittert 2002). Most humid areas were colonized by ferns with the lowest co-occurrences, forming monospecific thickets such as *T. brauniana*, *P. angustiloba*, *M. braunii*, *T. princeps*, *T. goeppertianus*, and *C. haiburnensis*. Among them are both herbaceous and arborescent forms. A second group with low co-occurrences and herbaceous taxa with very large fronds occupied the less humid environments (*C. roessertii* clusters in the same group, but had different

preferences). These forms co-occur mainly with *N. obtusa* and *Sagenopteris* sp.; only *C. meniscoides* shows higher associations with *Komlopteris nordenskioeldii* and *Elatocladus* sp. Since the co-occurrences are relatively low, it is probable that they formed also monospecific bushes, but in mixed communities.

Three taxa have separate positions on the PCA plot and are mostly co-occurring with other plants. *M. hoerensis*, although considered as a member of group 2, occupies a separate position within the group due to its high association with *N. obtusa* and *Sagenopteris* sp., and less frequent association with *K. nordenskioeldii*, *A. marginatus* and *Equisetites* sp. Considering *N. obtusa* as a rather small plant, whereas the morphology of *Sagenopteris* is unclear, and *M. hoerensis* having wide fronds, it is highly probable that the fern formed larger clumps within mixed assemblages. *C. denticulata*, a tree fern, was associated with *N. obtusa* in highest degree (three times more than *M. hoerensis*). It seems that *N. obtusa* is an indicator of dry environments. *C. denticulata* is one of the most commonly co-occurring fern species, confirming that this fern was more related to other plants within the community. The fern with the highest co-occurrence with other taxa, and the only one associated with ginkgophytes, is *P. kirchneri*. This herbaceous plant was connected to less disturbed habitats. Since the associated plants include many trees, like ginkgophytes, *K. nordenskioeldii* (Barbacka and van Konijnenburg-van Cittert 1998), or *Elatocladus* sp., this fern may be attributed to the understorey.

The palaeoecology of ferns from the Mecsek Mts. is comparable to extant ferns growing in tropics and their life strategy. According to Sharp et al. (2010), ferns very often form extended bushes that can be stable for a long time, because some of them can inhibit with allelopathic exudates the growth of trees and other plants. Their living fronds create dense shadow and dry fronds together with thick rhizomes cover the soil, inhibiting dispersal of seeds and seedlings. Ferns can easily colonize and expand instable habitats with their rhizomes (floods provide areas for colonization). Ferns thus form dense and self-perpetuating populations that can last a long time (thousands of years) because they inhibit changes in species composition, increase stabilization of soil and produce soil. The reproductive strategy by spores and rooting of trunk buds guarantees expansive growing. Thick soil cover and slowly decomposing fronds or other organs have a long-term impact on succession and soil development (Sharp et al. 2010).

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